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THE FAMILY LITTORINIDAE IN THE INDO-PACIFIC

Part I. The Subfamily Littorininae

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torinidae, the list of recognized taxa on page 423 [05-267] contains the names of all valid species recognized by me in the various generic groups.

Family Characters

Abstract

The classification of tropical Indo-Pacific Littorinidae (Mollusca: Mesogastropoda: Littorininae) has been revised. Thirty four Recent and six Tertiary fossil species belonging to six generic groups are described, and/or redescribed, and figured. Complete systematic synonymies are given, together with discussions of relationships, biology and zoogeography. One new subgenus and two new subspecies are described; one new name is assigned. Spawn characteristics of Littorinidae are reviewed. A list is given of recognized taxa of world-wide Littorinidae belonging to the subfamily Littorininae.

Indo-Pacific Littorinidae

Representatives of the family Littorinidae are found in most regions of the world occupying habitats from relatively shallow waters below the intertidal zone to situations high above the sea where they may be wet only occasionally by spray. Certain species are unusual among marine gastropods in their ability to survive for long periods without immersion in sea water (Rosewater, 1963a). These species may be considered as living examples of some stages in the invasion of the land by marine snails. The genus *Cremnoconchus* Blanford, 1869, inhabits fresh water, although it is doubtful that it invaded that habitat from the sea. Although the present paper is mainly concerned with marine Indo-Pacific Lit-

torinidae are generalized mesogastropods, and members of the type-genus, *Littorina*, have nothing outstanding about their appearance. It is, perhaps, this generalized condition which helps to distinguish them from other closely related gastropod families which possess at least some prominent characteristics. "Typical" *Littorina*, best exemplified by the type-species *Littorina littorea* (Linné, 1758) (see pl. 326, figs. 1, 2) have thick-walled turbate shells, are usually non-umbilicate, and have paucispiral opercula, although members of the genus *Echininus* disregard the general rule and have umbilicate shells and multispiral opercula. Sculpture varies from nearly smooth to spirally striate, axially furrowed, or nodulose. Some species of *Tectarius* are quite elaborately sculptured.

The anatomy of *Littorina* was described in some detail by Fretter and Graham (1962, see our pl. 327, figs. A and B). There is a moderately-sized, ditaxic foot bearing the operculum on its dorsal posterior surface; a head with two tentacles having dark eyes at their outer bases; a central, anterior snout with the mouth at its extremity. All species in the family so far as is known are dioecious; the male bears a penis and the female has a well-marked groove on the side of the "neck" for passage of eggs. Fertilization is internal, and pelagic development is the rule, although several species have evolved ovoviviparity. Species differences may be noted in penile anatomy, reproductive habits and characters of egg capsules (see table).



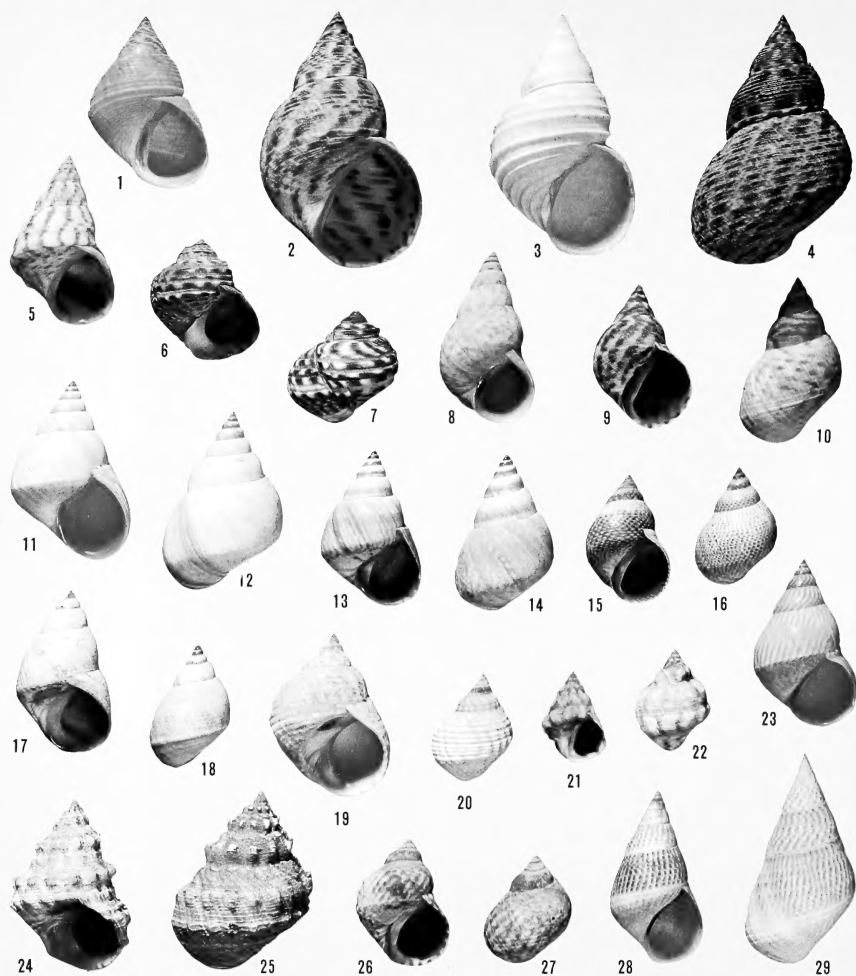


Plate 325. Subfamily Littorininae (explanation on opposite page).
(all figures about natural size)

Littorinidae most often are confused with such families as Planaxidae. The resemblance between the two is considerable but superficial. This confusion may be dispelled if it is remembered that the columella of Planaxidae terminates in a short, "pinched" siphon, while that of Littorinidae is always simple. The closest marine relative, Lacunidae, is readily recognized, due to the omnipresent umbilical chink, usually more conical shells, and metapodial tentacles. Details of habitat and reproductive characters are also different. Other possible *Littorina* "look-alikes" may be found among the Fossaridae and Trochacea and also in certain land and freshwater prosobranch families, such as the Helicinidae and Hydrobiidae. The latter do not, of course, occur in a habitat similar to that occupied by Littorinidae. Trochacea differ significantly in having the interior of the shell nacreous and also in being quite different anatomically.

Throughout the descriptions of the species, measurements of shell size are given in both millimeters and inches. The maximum length to which shells grow is given. The factor of obesity was determined by dividing the width of the shell by the length.

Spawn Characteristics

A review of the literature on reproduction in Littorinidae reveals that most species, about which the information is known, release pelagic capsules. A few deposit egg masses on a suitable substrate and produce living young. Below is a partial list of species, arranged according to

spawn type and faunal region. Following each species I have given the references and, where necessary, the correct name in square brackets.

A. Pelagic Capsule—

Indo-Pacific: *Littorina brevicula*: Kojima (1957, 1958a); Habe (1958); Yamamoto and Habe (1962); Hirai (1963); Yamaguchi (1967). *L. coccinea* (personal observations, see under *Description of L. coccinea*). *L. pintado*: Ostergaard (1950); Whipple (1965); Struhsaker (1966). *L. strigata* [= *L. undulata*?]: Kojima (1958c); *L. undulata* (personal observations, see *Description of L. undulata*). *Nodilittorina pyramidalis*: Kojima (1958b). *Granulilittorina granularis* [= *G. millegrana*]: Tokioka and Habe (1953); Habe (1955); Yamamoto and Habe (1962); Hirai (1963). *G. picta*: Whipple (1965); Struhsaker (1966, 1968b).

North Pacific: *Littorina squalida*: Habe (1958); Kojima (1958b, e); Yamamoto and Habe (1962).

Eastern Pacific: *Littorina planaxis*: MacGinitie and MacGinitie (1949), Gibson (1964).

Western and Eastern Atlantic: *Littorina littorea*: Thorsen (1946).

Eastern Atlantic: *Littorina neritoides*: Lebour (1935).

Western Atlantic: *Littorina ziczac*: Lebour (1945); Abbott (1954); Lewis (1960); Marcus and Marcus (1963); Borkowski (1969). *L. flava*: Marcus and Marcus (1963). *L. lineata*: Borkowski (1969). *L. lineolata*: Borkowski (1969). *L. meleagris*: Lewis (1960). *Nodilittorina tuberculata*: Lebour (1945); Abbott (1954); Lewis (1960). *Tectarius muricatus*: Lebour (1945); Abbott (1954); Lewis (1960).

Explanation to plate 325 (opposite page)

Figs. 1-4. *Littorina (Littorinopsis) scabra scabra* (Linné), showing some of the variation in color and form exhibited by the shell of this species. 1. from Pulau Hantu, SW of Keppel Harbor, Singapore (USNM 660841); 2. from Candaranan Id., Balabac, Philippines (USNM 233258); 3. from N. Queensland, Australia (USNM 149898); 4. from Bohaydulung Id., North Borneo (USNM 658031).

Fig. 5. *Littorina (Littorinopsis) carinifera* (Menke) from Bombay, India (USNM 90470).

Figs. 6, 7. *Littorina brevicula* (Philippi) from Awaji, Japan (USNM 343538).

Figs. 8-10. *Littorina (Littoraria) undulata* Gray. 8. from Pulau Nias, SW Sumatra, Indonesia (USNM 654451); 9, 10. from N. shore of Guadalcanal Id., Solomon Ids. (USNM 598188).

Figs. 11, 12. *Littorina (Littoraria) coccinea* (Gmelin) from SW Viti Levu, Fiji (USNM 531795).

Figs. 13, 14. *Littorina (Littoraria) mauritiana* (Lamarck) from Mauritius (USNM 26744).

Figs. 15, 16. *Littorina (Littoraria) pintado pintado* (Wood) from Hilo, Hawaii (USNM 339401).

Figs. 17, 18. *Littorina (Austrolittorina) unifasciata unifasciata* Gray. 17. from Port Jackson, New South Wales (USNM 89472); 18. from Kalbarri, Western Australia (USNM 691672).

Figs. 19, 20. *Nodilittorina australis* (Gray). 19. from Rottne Id., Western Australia (USNM 671214); 20. from Port Denison, Western Australia (USNM 691677).

Figs. 21, 22. *Nodilittorina nodosa* (Gray). 21. from "Western Australia" (USNM 679494); 22. from Kalbarri, Western Australia (USNM 691680).

Fig. 23. *Littorina (Littoraria) kraussi* Rosewater, from Mauritius (USNM 89410).

Figs. 24, 25. *Nodilittorina pyramidalis* (Quoy and Gaimard) from Lord Howe Id., off New South Wales, Australia (USNM 684715).

Figs. 26, 27. *Littorina (Littoraria) praetermissa* May from Port Fairy, Victoria, Australia (USNM 637353).

Figs. 28, 29. *Littorina (Littorinopsis) melanostoma* Gray. 28. from Pulau Lumut, Port Swettenham, Malaysia (USNM 661028); 29. from Kranji, Singapore (USNM 631930).

B. Egg Mass—

North and Northeastern Pacific: *Littorina atkana*: Kojima (1958a, d); Habe (1958). *L. sitkana*: Habe (1958); Yamamoto and Habe (1962).

Western and Eastern Atlantic: *Littorina obtusata*: Thorson (1946).

C. Ovoviviparous—

Indo-Pacific: *Littorina scabra scabra*: Whipple (1965); Struhsaker (1966).

Eastern and Western Atlantic: *L. scabra angulifera*: Lebour (1945); Lenderking (1954); Marcus and Marcus (1963). *L. saxatilis*: Thorson (1946).

In general, based on available information, most members of the subgenera *Littorina s.s.* and *Littoraria* produce a plano-convex or bi-convex egg capsule, containing from one to a dozen or so eggs (*L. littorea*, *brevicula*, *squalida*, *undulata*, *coccinea*, *pintado*). Information regarding the nature of the capsule is lacking for some species, such as *L. planaxis*. In the cases of *L. obtusata*, *sitkana* and *atkana* an egg mass is deposited on the substrate and, of course, *L. saxatilis* is ovoviviparous. Members of the subgenus *Littorinopsis* for which data are available are also ovoviviparous. In *Austrolittorina* and *Nodilittorina* rather

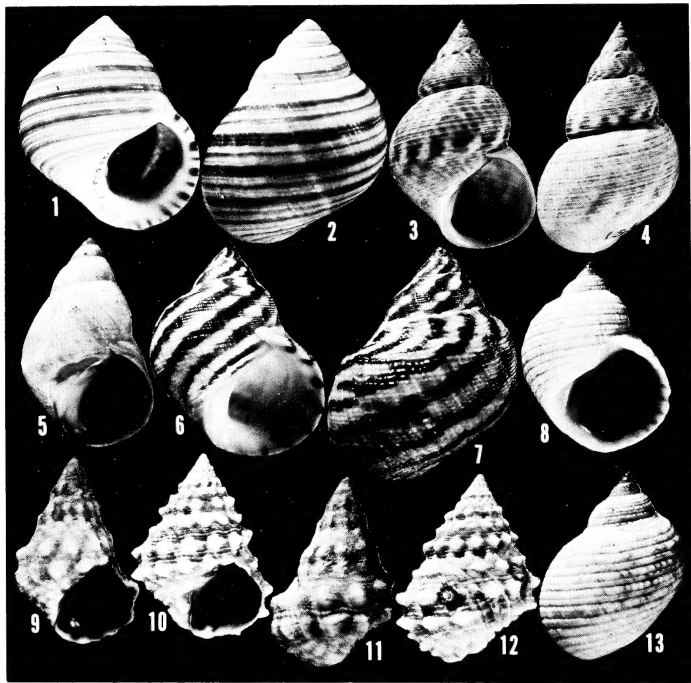


Plate 326. Type-species of Genera included in Indo-Pacific Littorinidae, Part I.

Figs. 1,2. *Littorina (Littorina) littorea* (Linné, 1758); specimen figured in J. C. Jeffreys, 1865, British Conchology, Vol. 3, pl. 8, fig 3 (Jeffreys Collection, USNM 185523; 29.7 × 21.3 mm.)

Figs. 3,4. *Littorina (Littorinopsis) angulifera* (Lamarck, 1822) from Sabanilla, Colombia (USNM 103151; 34.1 × 19.1 mm.)

Fig. 5. *Littorina (Austrolittorina) unifasciata unifasciata* (Gray, 1826) from Port Jackson, Australia (USNM 89472; 20.9 × 12 mm.; for abapertural view see pl. 359, fig. 2).

Figs. 6,7. *Littorina (Littoraria) zebra* (Donovan, 1825) from

Venado River, Panama Canal Zone (USNM 589696; 29.6 × 19.9 mm.)

Figs. 8,13. *Nodilittorina (Granulilittorina) millegrana* (Philippi, 1848) from Pulau Jerak, West of Sembilan Islands, Malaysia (USNM 661049; 12.1 × 8 mm.).

Figs. 9,11. *Nodilittorina (Nodilittorina) pyramidalis* (Quoy and Gaimard, 1832) from Airport Beach, Barrow Island, Western Australia (USNM 691681; 11.9 × 7.2 mm.)

Figs. 10,12. *Nodilittorina (Echinolittorina) tuberculata* (Menke, 1828) from Perme, northwest of Cape Tiburón, Atlantic coast of Panama (USNM 664217; 16.4 × 11 mm.) [included for comparison, although there are no Indo-Specific species].

elaborate "gear-decorated" or "terraced" capsules are produced. Of the three species whose egg capsules are known in *Melarhaphe*, one produces a flattened cylinder-shaped capsule (*L. neritoides*) another a tiered capsule (*L. meleagris*) and the third a biconvex capsule (*L. flava*) [the generic assignments of the last two forms is still questionable]. *Tectarius muricatus* produces a capsule which is rather like that of *L. neritoides*, but is biconvex.

A definite systematic trend in the shapes of littorinid egg capsules does not seem to exist

above the species level. It does appear, however, that each species has fairly characteristic spawn.

Radulae

The radulae of Littorinidae may be described as generalized taenioglossate (see pl. 328). So far as is known most species browse on the epiphytes of the hard substrates upon which they live. The radulae are adapted for scraping off this food and may become very long as considerable replacement of worn teeth is required. The unused portion is carried coiled up in the radula sac behind the head. Radulae of *Littorina* and its subgenera are all fairly similar, having the formula 2-1-1-1-2, and consisting of a slender multicuspoid outer marginal, (pl. 328 D) a more robust inner marginal (pl. 328 C), a subquadrate lateral with a basal embayment (the embayment is characteristic of Littorinidae) (pl. 328B), and a rachidian or central which is typically about as high as it is wide and which bears 3 cusps. In *Nodilittorina* and *Tectarius* there is a tendency for narrowing of the central tooth although the lateral and marginals are quite similar to the condition in *Littorina*. In the genus *Echininus* and especially its subgenus *Tectininus*, as shown by Abbott (1954), there is considerable reduction in width of both central and lateral teeth. Since most members of the Littorinidae apparently share the generalized taenioglossate radula and squarish lateral teeth, it does not seem to offer much promise for systematic diagnosis below the generic level.

Distribution

Most Littorinidae inhabit tropical seas, and the largest numbers of species live in the Indo-Pacific region. A conservative estimate places the total number of Recent world-wide Littorinidae of all genera at slightly above 100 species, excluding the freshwater representatives which at least may be considered a separate subfamily of the Littorinacea as may the members of the Rissel-

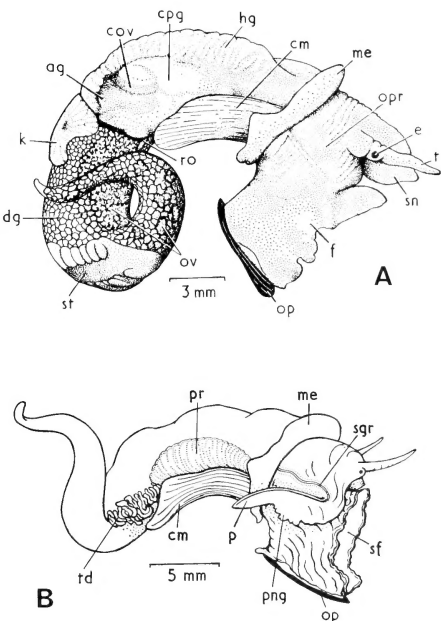


Plate 327. *Littorina littorea* (Linne) removed from shell showing right side of body of A. female; B. male (from Fretter and Graham, 1962).

Abbreviations—

ag,	albumen gland	ov,	ovary
cm,	columellar muscle	p,	penis
cov,	covering gland	png,	penial glands
cpg,	capsule gland	pr,	prostate
dg,	digestive gland	ro,	renal section of oviduct
e,	eye	sf,	sole of foot
f,	foot	sgr,	sperm groove
hg,	hypobranchial gland	sn,	snout
k,	kidney	st,	stomach
me,	mantle edge	t,	tentacle
op,	operculum	td,	testicular duct acting as vesicula seminalis
opr,	ovipositor		

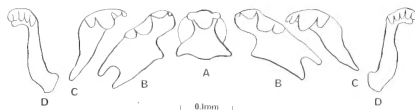


Plate 328. Radula of *Littorina littorea* (Linne), type-species of the genus *Littorina*. One complete transverse row of many which make up radula ribbon. Fig. A. rachidian or central tooth; Fig. B. lateral tooth C. and D. inner and outer marginal teeth.

lidae. Of these, some 34 species are to be found in the tropical Indo-Pacific, 21 inhabit the eastern Pacific, 16 the western Atlantic, only 9 the eastern Atlantic (5 of which are shared with the western Atlantic) and 27 more or less have been enumerated in the South Ocean (Antarctic) (see List of Recognized Taxa). Representatives of the family are conspicuously absent from the southern tip of South America. The distributional pattern is further complicated by the present in two or more regions of what are termed analogues, species which bear considerable resemblance and may be related (Rosewater, 1963b). Since the geologic history of the Littorinidae dates from the Jurassic, it is doubtful that origins of the family can be unraveled. Dispersal of species is aided now and undoubtedly was helped in the past by pelagic larvae and the semi-arboreal habitat of such species as *L. scabra*. A single fertilized female of the latter oviparous species, if rafted to a favorable locality, could establish a new colony.

Classification

Adapted as they are for intertidal life, it is not surprising to find little variation in general pattern of littorinid speciation. The shells are usually rounded-turbinate or some modification of this shape, permitting the animals to cling to rocks in surf or creep into crevices to avoid desiccation. Grossly, the animals which form the shells do not vary much either. The systematists' task of classifying species and groups of species into genera has come to depend on consistent differences in shape and sculpture and outstanding differences in anatomical details. Characters which have been utilized most in the present study are absence or presence of nodulosity and granulate sculpture, overall color pattern and shape, the radula, and penile anatomy. The latter character appears to be an extremely important and reliable one, and two levels of classification have been based on it, at least in part: 1) the separation of species and 2) the formation of species groups (genera) exhibiting overall similarity in penile anatomy and other features.

Difficulties have been encountered in the classification of fossils. As mentioned previously, shells of Littorinidae resemble those of a number of other marine, freshwater and land prosobranchs. If fossil preservation is not good, the decision on familial placement is extremely difficult, if not impossible. Even if preservation is optimum, since there are no anatomical characters upon which to rely, one can almost never be sure that these assignments are correct. This is

especially true of the older fossils where resemblance to Littorinidae is rather nebulous. For these reasons much concerning fossils has been taken on faith and must be regarded in that light. Only Tertiary Indo-Pacific fossils are included here or listed in the List of Recognized Taxa.

As is the case with many groups of animals, not alone mollusks, an ample number of species and genera have been described in the Littorinidae. In many cases these are not justified in the light of modern systematics and some have had to be synonymized. Early in the course of this study it was thought probable that most of the generic names erected for species originally described or early assigned to *Littorina* would be of little value. After long evaluation, it has become apparent that some of these names may have real utility, at least as subgeneric groups indicators and it may be noted that they are so used throughout. It is hoped that in each case the reason for their use will be made clear.

List of Recognized Taxa

The following is a list of recognized species, subgenera and genera of world Littorinidae belonging to the subfamily Littorininae. Fossils listed are Tertiary forms described from the Indo-Pacific region alone; the sheer numbers and the uncertainties surrounding extraterritorial and pre-Tertiary fossil species preclude their consideration here. As mentioned previously, the generic groupings are controversial but are offered as a working solution to some method of orderly arrangement of species. Due to the means of presentation many possibly familiar names will be missed by some in the list. Often they are considered to be synonyms and in the cases of Indo-Pacific species are included in the synonymies which follow. The few fossil species names are preceded by a dagger [†].

Certain littorinoid groups, although definitely "Indo-Pacific" in general geography, are not considered here. These are the members of such genera as *Bembicium* and *Peasiella* here believed to constitute at least a separate subfamily of Littorinidae. I consider the freshwater forms, such as *Cremnoconchus* and *Cremnobates*, also to be separable as at least a subfamily. Forms having definite southern ocean affinities, inhabiting New Zealand and the Antarctic, such as *Laevilitorina*, *Macquariella*, etc., are included in the list of recognized taxa, but will not be considered in detail here. A second part of Indo-Pacific Littorinidae, covering the subfamilies Tectariinae and Echininae will appear at some future time.

Family Littorinidae Gray, 1840

Subfamily Littorininae

GENUS *Littorina* Ferussac, 1822Subgenus *Littorina* Ferussac, 1822.

littorea (Linné, 1758).

Type. Recent, North Atlantic
obtusata (Linné, 1758). Recent, North Atlantic

saxatilis (Olivi, 1792). Recent, circumboreal
sitkana Philippi, 1846. Recent, northeast Pacific

atkana Dall, 1886. Recent, North Pacific
aleutica Dall, 1872. Recent, North Pacific
squalida Broderip & Sowerby, 1829. Recent, North Pacific

brevicula (Philippi, 1844).

Recent; East Asia, Japan

planaxis Philippi, 1847. Recent, northeast Pacific

scutulata Gould, 1849. Recent, northeast Pacific

ziczac (Gmelin, 1791). Recent; tropical western Atlantic

Subgenus *Littoraria* Gray, 1834

zebra (Donovan, 1825). **Type.** Recent, tropical eastern Pacific

undulata Gray, 1839. Recent, Indo-Pacific
nebulosa (Lamarck, 1822). Recent, Caribbean and Gulf of Mexico

mauritiana (Lamarck, 1822). Recent, Indian Ocean

kraussi Rosewater, *new name* Recent, Indian Ocean

coccinea (Gmelin, 1791) Recent; Indo-Pacific

praetermissa May, 1909. Recent, South Australia

pintado (Wood, 1828). Recent; Indo-Pacific
pintado schmitti, Bartsch & Rehder, 1939. Recent, Clipperton Island

pullata Carpenter, 1864. Recent; tropical eastern Pacific

cingulifera Dunker 1845. Recent; tropical west Africa

?*sundaica* Altena, 1945. Recent, Java

?*acutispira* E. A. Smith, 1892. Recent, Australia

?*infans* E. A. Smith, 1892. Recent, Australia

†*kozaiensis* Nomura and Onisi, 1940. Miocene, Japan

†*adonis* Yokoyama, 1927. Pliocene, Japan

†*lucida* Yokoyama, 1927. Pliocene, Japan

Subgenus *Littorinopsis* Mörch, 1876

scabra scabra (Linne, 1758). Recent, Indo-Pacific

scabra angulifera (Lamarck, 1822). **Type.**

Recent, eastern and western Atlantic

scabra aberrans Philippi, 1846. Recent, tropical east Pacific

melanostoma Gray, 1839. Recent, south Asia.

carinifera (Menke, 1830). Recent, Indo-Pacific

irrorata (Say, 1822). Recent, western Atlantic

fasciata Gray, 1839. Recent, tropical east Pacific

varia Sowerby, 1832. Recent, tropical east Pacific

modesta Philippi, 1846. Recent, tropical east Pacific

paytensis Philippi, 1847. Recent, tropical east Pacific

†*miodelicatulata* Oyama, 1950. Miocene, Japan.

†*incisa* Yokoyama, 1927. Pliocene, Japan.

Subgenus *Austrolittorina* Rosewater, *new subgenus*

unifasciata unifasciata Gray, 1826. **Type.** Recent, Australia

unifasciata antipoda Philippi, 1847. Recent, New Zealand

unifasciata fernandezensis Rosewater *new subspecies*. Recent, Islas Juan Fernandez

cincta Quoy and Gaimard, 1832. Recent, New Zealand

araucana Orbigny, 1840. Recent, Chili and Peru

peruviana (Lamarck, 1822). Recent, south-eastern Pacific

aspera Philippi, 1846. Recent, tropical east Pacific

penicillata Carpenter, 1864. Recent, Baja California

tessellata Philippi, 1847. Recent, Caribbean

lineata Orbigny, 1841. Recent, tropical western Atlantic

lineolata Orbigny, 1840. Recent, tropical western Atlantic

punctata (Gmelin, 1791). Recent, East Atlantic and South Africa

africana Philippi, 1847. Recent, South Africa

knysnaensis Philippi, 1847. Recent, South Africa

Subgenus **Melarthaphe** Menke, 1828

neritoides (Linne, 1758) **Type.** Recent, east Atlantic

?*mespillum* (Muhlfeld, 1824). Recent, tropical western Atlantic

?*meleagris* (Potiez and Michaud, 1838) Recent, West Indies

?*umbilicata* Orbigny, 1840. Recent, Chili and Peru

?*flava* King and Broderip, 1832. Recent, tropical west Atlantic

Subgenus **Algamorda** Dall, 1918

newcombiana (Hemphill, 1877). **Type.** Recent, northwest North America

GENUS **Nodilittorina** von Martens, 1897Subgenus **Nodilittorina** von Martens, 1897

pyramidalis pyramidalis (Quoy and Gaimard, 1833).

Type. Recent, Indo-Pacific.

pyramidalis pascua Rosewater, new subspecies. Recent, Easter and Pitcairn Islands.
natalensis (Philippi, 1847). Recent, East Africa and Madagascar.

australis (Gray, 1826). Recent, W. Australia.

nodosa (Gray, 1839). Recent W. Australia.

galapagensis (Stearns, 1892). Recent, Galapagos Islands.

Subgenus **Echinolittorina** Habe, 1956

tuberculata (Menke, 1828). **Type.** Recent, tropical west Atlantic.

Subgenus **Granulilittorina** Habe and Kosuge, 1966

millegrana (Philippi, 1948). **Type.** Recent, Indo-Pacific.

subnodosa (Philippi, 1847). Recent, Red Sea and Persian Gulf.

leucosticta leucosticta (Philippi, 1847). Recent, India.

leucosticta biangulata (von Martens, 1897). Recent, east Indies and western Melanesia.

leucosticta feejeensis (Reeve, 1857). Recent, western Pacific.

exigua (Dunker, 1860). Recent, Japan.

†*wakiana* (Nomura and Hatai, 1936). Miocene, Japan.

cinerea (Pease, 1869). Recent, Marquesas Islands

picta (Philippi, 1846). Recent, Hawaii.

?*miliaris* (Quoy and Gaimard, 1833). Recent, east Atlantic

?*striata* (King and Broderip, 1832). Recent, east Atlantic

GENUS **Laevilittorina** Pfeffer, 1886Subgenus **Laevilittorina** Pfeffer, 1886

caliginosa caliginosa (Gould, 1849). **Type.** Recent, Southern Ocean

caliginosa aestualis Strebel, 1908. Recent, Antarctica

antipoda (Filhol, 1880) Recent, New Zealand

bifasciata Suter, 1913. Recent, New Zealand

bennetti Preston, 1912. Recent, Antarctic

claviformis Preston, 1916. Recent, Antarctic

granum Pfeffer in von Martens & Pfeffer, 1886. Recent, Antarctic

littorina Preston, 1912. Recent, Antarctic

pygmaea Pfeffer, 1886. Recent, Antarctic

umbilicata Pfeffer, 1886. Recent, Antarctic

venusta Pfeffer, 1886. Recent, Antarctic

antarctica E. A. Smith, 1902. Recent, Antarctic

Subgenus **Corneolittorina** Powell, 1951

coriacea (Melvill and Standen, 1907). **Type.** Recent, Antarctic

elongata Pelseneer, 1903. Recent, Antarctic

heardensis Dell, 1964. Recent, Antarctic

GENUS **Macquariella** Finlay, 1926

hamiltoni (Smith, 1898). **Type.** Recent, New Zealand

aucklandica Powell, 1933. Recent, New Zealand

delli Powell, 1955. Recent, New Zealand

macphersonae Dell, 1964. Recent, Macquarie Island

GENUS **Laevilacunaria** Powell, 1951Subgenus **Laevilacunaria** Powell, 1951

bransfieldensis (Preston, 1916). **Type.** Recent, Antarctic

antarctica (von Martens, 1885). Recent, Antarctic

pumilio (E. A. Smith, 1879). Recent, Antarctic

Subgenus **Pellilacunella** Powell, 1951

bennetti (Preston, 1916). **Type.** Recent, Antarctic

GENUS *Pellilitorina* Pfeffer, 1886

setosa (Smith, 1875). **Type.** Recent, Antarctic
pellita (von Martens, 1885) Recent, Antarctic

GENUS *Rissolittorina* Ponder, 1966

alta (Powell, 1940). **Type.** Recent, New Zealand
mariae (Tenison-Woods, 1876). Recent, Tasmania

Abbreviations

The following institutional abbreviations are used in this paper:

AMS-Australian Museum, Sydney
 ANSP-Academy of Natural Sciences of Philadelphia
 BM(NH)-British Museum (Natural History), London
 BPBM-Bernice P. Bishop Museum, Honolulu
 MHNG-Muséum d'Histoire Naturelle, Geneva
 MHNP-Muséum d'Histoire Naturelle, Paris
 MCZ-Museum of Comparative Zoology, Cambridge, Massachusetts
 NMW-National Museum of Wales, Cardiff
 RNHL-Rijksmuseum van Natuurlijke Historie, Leiden
 SMF-Senckenberg Museum, Frankfurt-am-Main
 USNM-United States National Museum, Washington, D.C.
 WAM-Western Australian Museum, Perth, Western Australia
 YPM-Peabody Museum of Natural History, Yale University, New Haven, Connecticut
 ZMA-Zoological Museum, Amsterdam
 ZMC-Zoological Museum, Copenhagen

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Doubtful Species of Littorinidae

Included under this heading are species of Littorinidae from the Indo-Pacific which I consider either unrecognizable as valid species from the faunal area, or as being questionably included in the family. In the latter category, some species already have been removed from the family by prior workers. Although Iredale and McMichael (1962) listed *Larinopsis turbinata* (Gatliff and Gabriel, 1909) and *L. ostensus* Iredale, 1936, in Littorinidae, the genus *Larinopsis* Gatliff and Gabriel, 1916, was placed in Fossaridae by Wenz (1940) and by Macpherson and Gabriel (1962, including the mentioned species). Ponder (1966) has shown that some species placed in *Zelaxitas*, formerly thought to be Littorinidae, belong to three different families, that genus now being assigned to Rissoidae. Only one species originally included under *Zelaxitas*, *Z. alta* Powell, 1940, remains in Littorinidae, although in a different genus (see List of Recognized Taxa under *Rissolittorina* Ponder).

Littorina beccarii Tapparone-Canefri, 1875

Range—Known only from the type-locality: Sorong, northwest New Guinea (West Irian, Indonesia).

Remarks—This species has not been figured and its identity is in doubt. The author's suggestion that an affinity exists with *Littorina lamellosa* Montrouzier indicates that it is a *Fossarus* and not a *Littorina*. Mrs. van Benthem Jutting (1962) published the results of her studies on the types of New Guinea non-marine mollusks described by Tapparone-Canefri. These were preserved in the Genoa Museum, and it is possible that the type of *L. beccarii* is there also. Unfortunately it has not been possible to ascertain this fact in the course of the present study.

Synonymy—

- 1875 *Littorina beccarii* Tapparone-Canefri, *Annali del Museo civico di Storia Naturale di Genova*, vol. 7, p. 1031 (Sorong [N.W. New Guinea]).

Littorina fragilis Fenaux, 1943

Remarks—The illustration accompanying the description of this species indicates that it is very probably a member of the genus *Diala* (Cerithiidae) and not a *Littorina*.

Synonymy—

- 1943 *Littorina fragilis* Fenaux, *Bulletin de l'Institut océanographique*, Monaco, no. 835, p. 7, figs. 4, 5 (Pau-motou).

Problitora globulus (Angas, 1880)

Remarks—Macpherson and Gabriel (1962) placed this species in the genus *Problitora* Iredale, 1931, of which *P. moerchi* (Adams and Angas) is the type-species. As *globulus* was described from shell-sand, and has been collected on only very few occasions, its true relationships remain to be proven. At present there appears to be little reason for retaining these peculiar forms in the family Littorinidae as they resemble much more closely members of the family Naticidae.

Synonymy—

- 1880 *Amauropis globulus* Angas, *Proceedings of the Zoological Society of London*, 1880, part 3, p. 416, pl. 40, fig. 5 (Holdfast Bay in shell-sand [near Adelaide, South Australia]); types, BM(NH) 81.4.29.5.

Littorina hisseyiana Tenison-Woods, 1876

Remarks—May (1903) figured the type of *L. hisseyiana*. His illustration shows a tiny, apparently umbilicated snail with a multispiral operculum, and having a color pattern resembling

one of the Trochacea. It is certainly not a *Littorina*.

Synonymy—

- 1876 *Littorina hisseyiana* Tenison-Woods, *Papers and Proceedings of the Royal Society of Tasmania*, for 1875, p. 148 (from stomach of a mullet, *Agenostoma die-menensis* Rich, probably caught in the Derwent [Tasmania]). 1903, W. L. May, *ibid.*, for 1902, p. 111, fig. 7; 7 syntypes in Tasmanian Museum (T.M. 5480) according to Hardy, 1916, *ibid.*, for 1915, p. 66.

Littorina lamellosa Montrouzier, 1861

Remarks—Although described as a *Littorina*, the author observed that this species resembles a fossarid. This is certainly the case, as the original illustration almost exactly matches the Hawaiian species which was named by Pease as *Fossarus garretti*.

Synonymy—

- 1861 *Littorina lamellosa* Montrouzier, *Journal de Conchyliologie*, vol. 9, p. 273, pl. 11, fig. 5 ([Ille] Art, New Caledonia).

Problitora moerchi (Adams and Angas, 1864)

Remarks—See Remarks under *P. globulus* (Angas). I consider this species not to belong in Littorinidae. The figures by Hedley (1902) especially that of the operculum, resemble more closely one of the Naticidae.

Synonymy—

- 1864 *Amauropis moerchi* Adams and Angas, *Proceedings of the Zoological Society of London*, 1863, part 3, p. 423 (Watson's Bay, Port Jackson [New South Wales]); type, BM(NH) 70.10.26.178. 1902, Hedley, *Proceedings of the Linnean Society of New South Wales*, vol. 26, part 4, p. 700, pl. 34, figs. 19, 20.

Littorina reticulata Anton, 1839

Remarks—Anton's species could be any of several *Granulilittorina*. The description and Philippi's figure are too vague to identify the species with any precision and the lack of a locality increases the likelihood that *L. reticulata* may be an extra-Indo-Pacific entity. The species is here considered unrecognized.

Synonymy—

- 1839 *Littorina reticulata* Anton, *Verzeichniss der Conchylien welche sich in der Sammlung von H. E. Anton befinden*. Halle, p. 53 (no locality given). 1847, Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, p. 199, pl. 4, fig. 12 [figure said to be drawn from one of Anton's type-specimens].

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Subfamily Littorininae Gray, 1840

Key To Subgeneric Groups of Indo-Pacific Littorininae

The following key is an attempt to provide a point of departure for the placement of a littorinid species in a particular subgeneric group. Even at the generic level there is a great deal of phenotypic variation expressed and it is often true that such hopefully dependable characters as nodular and granular sculpture are evanescent. Other keys are provided in the appropriate places to species of *Littoraria* and *Littorinopsis*. None are provided for the other groups, however, be-

cause it was felt that species of *Austrolittorina* and *Nodilittorina* s.s. are sufficiently distinct and geographically situated so as to essentially preclude difficulties in identification. In the case of *Granulilittorina*, the nature of speciation in the group makes the construction of an effective key a near impossibility. It is suggested that the user may wish to acquire some familiarity with the range of variation in this subfamily before proceeding.

1. Shell nodulose, granulose, or with surface axially folded 2
1. Shell surface smooth or spirally folded (carinate) 3
2. Sculpture nodulose, limited to 2-3 rows per whorl of major nodules, or surface axially folded *Nodilittorina* p. 05-375
2. Sculpture granulose, often in excess of 3 rows of granulations, sometimes nearly smooth *Granulilittorina* p. 05-395
3. Base of shell adjacent to columella flattened or hollowed out, forming a crescent-shaped area *Austrolittorina* p. 05-351
3. Base of shell adjacent to columella generally smoothly rounded, not flattened or hollowed out 4
4. Spire less than half the length of shell, multiple penial glands present *Littorina* p. 05-285
4. Spire usually more than half the length of shell, penial glands absent 5
5. Shell rather thin for its size, conspicuously colored or patterned, usually arboreal or plant-living species *Littorinopsis* p. 05-329
5. Shell not thin for its size, often with subdued coloration or lacking pattern, usually rock-living species *Littoraria* p. 05-297

Family Littorinidae Gray, 1840

Subfamily Littorininae Gray, 1840

Genus *Littorina* Férussac, 1822

Type: *Littorina littorea* (Linné, 1758)

Considered broadly, the genus *Littorina* encompasses a multitude of Recent and fossil species throughout the world. The impossibility of properly classifying the large number of poorly preserved fossil species described from the Upper Paleozoic through the Tertiary prevents coverage here of any but Tertiary Indo-Pacific fossils. Living species of the genus *Littorina* usually occupy habitats on rocks in the intertidal zone although some species prefer shore vegetation. The geographic range of the genus is from Arctic to Antarctic shores, including intervening temperate and tropical areas where a suitable habitat is available. The subgenus *Littorina*, *sensu stricto*, however, is a northern group and there is only one species of that subgenus whose range extends into the tropical Indo-Pacific, *Littorina brevicula* (Philippi), which is treated here (see List of Recognized Taxa).

Synonymy—

- 1822 *Littorina* Férussac, Tableaux Systématiques des Animaux Mollusques, p. xxxiv. Type-species by subsequent designation, Blainville, 1828, Dictionnaire des Sciences Naturelles, Paris, vol. 56, p. 98: *Turbo littoreus* [= *Littorina littorea* (Linné)].
- 1827 *Littorina* 'Férussac' Nilsson, Petrificata Suecana Formationis Cretaceae, part 2, Mollusca, p. 11. Invalid type-species by monotypy: *Turbo sulcatus* Nilsson, 1827, a species not originally included by Férussac.
- 1827 *Neritoides* T. Brown, Illustrations of the Conchology of Great Britain and Ireland, Index p. iv, pl. 43, figs. 14, 15, 21, 22. Type-species by monotypy: *Neritoides littoralis* [= *Littorina obtusata* (Linné, 1758)].
- 1828 *Litorina* Menke, Synopsis Methodica Molluscorum, p. 24 [emendation of *Littorina* Férussac, 1822].
- 1847 *Littorelaea* Leach, Annals and Magazine of Natural History, vol. 20, p. 271; in combination *Littorelaea pulneyi* [nomen nudum].
- 1849 *Littorina* Mörch, Indbydelsesskrift til de offentlige afgangsgang-og aarsprøver i Nykjøbing katedralskole, p. 63 [error for *Littorina* Férussac, 1822].
- 1854 *Bacalia* H. and A. Adams, Genera of Recent and Fossil Mollusks, vol. 1, p. 312; based on *Bacalia* Gray, 1840, Synopsis of the Contents of the British Museum, ed. 42, p. 147 [nomen nudum]; type-species by subsequent designation, Winckworth, 1922: *Turbo littoreus* Linné.
- 1861 *Littorina* Gabb, Proceedings of the American Philosophical Society, vol. 8, p. 114 [error for *Littorina* Férussac, 1822].
- 1869 *Neritrema* Récluz, Actes de la Société Linnéenne de Bordeaux, series 3, vol. 7 (vol. 27) pp. 43, 46. Type-species by subsequent designation, Dall, 1909, U.S. Geological Survey Professional Paper 59, p. 79: *Littorina obtusata* Linné.
- 1878 *Litonia* Weinkauff, Systematisches Conchylien-Cabinet, vol. 2, part 9, p. 40 [error for *Littorina* Férussac, 1822].
- 1884 *Litorina* Dall, Proceedings U.S. National Museum, vol. 7, p. 344 [error for *Littorina* Férussac, 1822].
- 1891 *Isonema* 'Hall' Provancher, Faune Canadienne: Les Mollusques de la Province de Québec, part 1, p. 91. Type-species by subsequent designation Bequaert, 1943 *Johnsonia*, vol. 1, p. 1: *Turbo littoreus* Linné, 1758; not *Isonema* Meek and Worthen, 1866.
- 1891 *Littoria* Jenkins and Grocock, Hardwicke's Science Gossip, vol. 27, p. 9; 1917, H. B. Preston, Zoological Record, vol. 52, section 8, Mollusca, p. 33 [error for *Littorina* Férussac, 1822].
- 1918 *Algaroda* Dall, Proceedings of the Biological Society of Washington, vol. 31, p. 137; type-species by original designation: *Littorina littorea* Linné.
- 1918 *Littoriua* Dall, *ibid.*, Type-species by original designation: *Littorina sitchana* Philippi.
- 1939 *Neritotrema* 'Récluz' Wenz, Handbuch der Paläozoologie, Lief 4, Band 6, Gastropoda, part 3, Prosobranchia p. 518 [emendation of *Neritrema* Récluz, 1869].
- 1958 *Ezollittorina* Habe, Publications from the Akkeshi Marine Biological Station, no. 8, p. 9; type-species by monotypy: *Ezollittorina squalida* Broderip and Sowbery.

As has been accurately pointed out by Winckworth (1922) and Bequaert (1943) Férussac cited the names of several species in association with his description of *Littorina*. The "*Paludina* marine" listed on pages 9-11 of the introduction to Férussac's work are *obtusatus*, *neritoides*, *littoreus*, *muricatus* and *afer*. Following the list Férussac mentioned (p. 11) in vernacular "*littorine*" as a subgenus to contain some species previously assigned to *Turbo* and *Trochus*. In the following paragraph he assigned *Turbo neritoides* of Linné to this subgenus, at least in part. Since the latter cannot be construed as a type designation, it is necessary to seek a later one. Blainville (1824, Dictionnaire des Sciences Naturelles, Paris, vol. 32, p. 226) gave as an example of Férussac's "*Littorine*": *Turbo littoralis*, referring to Chemnitz vol. 5, t. 185, fig. 1852, nos. 1-18 [1-8] [figures are *L. littorea*]. This is an invalid subsequent designation (I.C.Z.N. Art. 69 (a) (i) and (iv)), and the same is true in the case of Payraudeau's (1826) description of *L. basterotii* [= *L. neritoides* (Linné)] in association with *Littorina*. The first valid designation is that of Blainville, (1828 *ibid.*) who clearly indicated *Turbo littoreus*, one of the originally included species as the type of the genus.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus *Littorina sensu stricto*

Characteristics of species belonging to the subgenus *Littorina s.s.* include a generally boreal distribution, relatively large, somber colored shells (with a number of exceptions) and the morphological character of the presence in the male of a series of penial glands with accessory flagella on the penis.

Littorina brevicula (Philippi, 1844)

(Pls. 325, 329, 330)

Range—Northern China, Korea and Japan (and boreal Pacific).

Remarks—*Littorina* (*Littorina*) *brevicula* is an inhabitant of the boreal Pacific. Although strictly a cool water species, it is included here with species occurring in the tropical Indo-Pacific because its range does extend to the southern most of Japan's main islands and also to the coast of China at latitudes roughly on a level with Taiwan. It occurs therefore within the range of a number of tropical species.

The anatomy of the penis of *L. brevicula*, which possesses multiple penial glands, the characteristics of the floating egg (helmet) capsule, which is a relatively simple plano-convex shape, the generalized radula and somber coloration of the shell all align this species with the boreal group of *Littorina s.s.*

Habitat—Intertidal on rocky coasts.

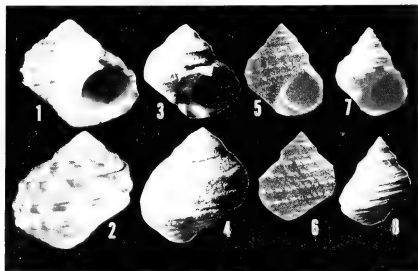


Plate 329. *Littorina brevicula* (Philippi).

Figs. 1,2. Specimens from Takami, Honshu, Japan (USNM 424296; 11.7×9.3 mm.).

Figs. 3,4. *Littorina souverbiana* Crosse, Holotype (Journal de Conchyliologie Collection, Paris Museum; 11.5×11 mm.).

Figs. 5,6. *Turbo* (*Littorina*) *breviculus* Philippi, lectotype figure (from 'Abbildungen und Beschreibungen Conchylien', vol. 2, p. 161, pl. 3, fig 10; about 11×10 mm.).

Figs. 7,8. *Littorina balteata* Reeve, lectotype (British Museum (NH) 1968316; 11×7.6 mm.).

Description—Shell reaching nearly 23 mm. (about 0.8 inch) in length, broadly-to depressed turbate in shape, often appearing almost as broad as long, but having an average obesity of about .74 (39 specimens range from .68-.79); rather thick in structure, imperforate; usually displaying an accentuated pointed siphonal trough; body whorl often sculptured with 3 or 4 raised strong, white-speckled spiral cords. External color variable; reddish brown to grayish white solid color or with banding, spotting, striping and zigzag color patterns. Aperture diffuse tan to brown with faint narrow white band revolving inward from near anterior junction of outer lip and columella, occasionally a wider, very diffuse band visible inside outer lip midway to its anterior junction with columella; columella grayish white anteriorly, merging with aperture color posteriorly; inner edge of outer lip often dark brown or speckled brown and white. Base distinctly flattened with comparatively low spiral cords; whorls broadly shouldered below suture. Whorls 4-5, rounded, nuclear whorls usually e-rod. Spire usually less than half the length of shell, produced at an angle varying from about 75° to 110° in very shortspired individuals. Aperture rounded-oval; inner and outer lips relatively thickly produced; with a distinctly pointed siphonal trough at anterior junction of outer lip and columella, often tinged with brown in young individuals; base adjacent to columella seldom depressed, but occasionally an anomalous umbilical chink formed. Suture impressed. Spiral sculpture usually consisting of from 3-4 major raised cords on upper half of body whorl; from

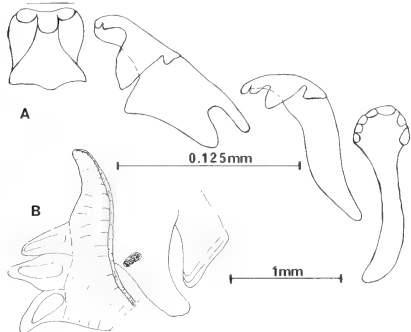


Plate 330. *Littorina brevicula* (Philippi).

Fig. A. Radula, showing central and one-half row of teeth (upper scale is 0.125 mm.); Hakodate, Japan.

Fig. B. Penis of young specimen from Wuchihsu, China (lower scale is 1 mm.).

4-6 minor cords on lower half on base; spire sculpture usually at least partially obliterated. Nuclear whorls about 2-2½, smooth, light-brown; post nuclear whorls rapidly becoming spirally sculptured with 1-2 cords. Overall microscopic sculpture consisting of fine wavy spiral threads especially noticeable between major cords, and fine, rather regular, oblique axial growth markings. Operculum roundly oval, paucispinal, the nucleus well defined and nearly central. Radula littorinoid, 2-1-1-1-2, the central tooth broad.

Animal darkly pigmented on surfaces of tentacles, snout and foot; the penis of small individuals (shell length 5-6 mm.) bearing 2 or 3 penial glands with accessory flagella. Reproduction oviparous, producing pelagic egg capsules, plano-convex in shape. The capsule measured about 350μ in maximum diameter and 170μ in height, the egg about 84μ in diameter, there being usually only 1 egg per capsule (Kojima, 1957). The breeding season was found to be from February to April at Asamushi, Japan.

Measurements (mm)—

length	width	no. whorls	locality
22.8	16.0	4	Hakodate, Japan
20.1	13.7	4+	Kamoiito, Teshiwo, Japan
19.3	15.2	4	Muroran, Japan
17.8	13.3	4	Muroran, Japan
16.2	12.0	4	Awaji, Japan
14.4	11.4	4	Muroran, Japan
12.6	9.2	5	Shirahama, Japan
11.2	8.5	3	Side Saddle Island, China
10.8	8.5	4	Cheefoo, China
9.3	6.8	4	Pei-tai-ho, China

Synonymy—

- 1844 *Turbo (Littorina) breviculus* Philippi, Zeitschrift für Malakozoologie, vol. 1, p. 166 (China, at mouth of Yang-tse-Kiang [Largilliert]); 1847, *Abbildungen und Beschreibungen* Conchyl., vol. 2, p. 161, *Littorina*, pl. 3, fig. 10. (lectotype figure).
- 1857 *Littorina balteata* Reeve, *Conchologia Iconica*, vol. 10, *Littorina*, pl. 14, fig. 71, a,b (China; lectotype BM(NH) 1968316: 11 x 7.6 mm.).
- 1861 *Littorina mandshurica* Schrenck, *Bulletin de L'Académie Impériale des Sciences de St. Pétersbourg*, vol. 4, no. 7, p. 409 (Sinus des Castris [Zaliv Chikhaeva, Gulf of Tartary, USSR]) type in Academy of Sciences Leningrad? 1867, *Reisen und Forschungen im Amur-Lande*, vol. 2, p. 333, pl. 14, figs 14-20.
- 1862 *Littorina souverbiana* Crosse, *Journal de Conchyliologie*, vol. 10, p. 53, pl. 1, figs 6-7 (in Sinu Taliwhanensi [North China]; holotype MHN: 13 x 10 mm).
- 1867 *Littorina mandshurica carinata* Schrenck, *Reisen und Forschungen im Amur-Lande*, vol. 2, p. 338 (no locality given).

- 1867 *Littorina mandshurica laevigata* Schrenck, *ibid.*
- 1887 *Littorina manshurica* 'Schrenck' Tryon, *Manual of Conchology*, vol. 9, pp. 241, 300 [error for *L. mandshurica* Schrenck].
- 1928 *Littorina heterospiralis* Grabau and King, *Shells of Peitaiho*, Peking Society of Natural History, Hand-book no. 2, second ed., p. 230, pl. 10, fig. 104 (Peitaiho [China]); types in Peking?

Types—The type specimen of *Turbo (Littorina) breviculus* Philippi may be in the Berlin Museum, although it has been impossible for me to determine this with certainty. The lectotype figure appears in *Abbildungen und Beschreibungen Conchyl.*, pl. 3, fig. 10 (see our pl. 329 figs. 5, 6). The lectotype of *Littorina balteata* Reeve is in the British Museum (NH)1968316. Types of *L. mandshurica* Schrenck and of its subspecies *carinata* and *laevigata*, may be in the Academy of Sciences, Leningrad. The holotype of *L. souverbiana* Cross is in the Paris Museum (Journal de Conchyliologie Collection). The type of *L. heterospiralis* Grabau and King, may be in Peking.

Records—KOREA: Wonsan Beach, Wonsan (MCZ); 2 mi. W. of Masan (USNM); Sorai (Sorai-men) (ANSP). CHINA: Port Arthur (Lu-shuh), Manchuria (ANSP, MCZ); Pei-tai-ho, N. Chihli coast; Cheefoo (Yen T'ai); Chiao-chou (Kiautschou), nr. Tsingtau (Isington). Yellow Sea; Side Saddle Island (Lu-Hua Shan), Che-Kiang Province; Foochow (Fu-chow) (all USNM); Wuchiu Hsu (ZMC). JAPAN: HONSHU: Kominato; Yenosima (Islands) (USNM, MCZ); Isu, Ise (Isu-shima?) (MCZ); Tokyo Bay (Yedo Bay) (USNM, MCZ); Tsukushima, Tokyo, Tokyo Bay (USNM, MCZ); Shirahama, Wakayama Prefecture; Yokohama (both ANSP, USNM); Misaki, Sagami Bay, off Hondo (USNM); Sagami Bay, Zushi Beach (MCZ); Shinagawa Bay, Tokyo; Toshima, Tanabe-wan, Seto Marine Biology Lab., Shirahama, Wakayama-ken (both USNM); Inland Sea (Seto-Naikai) (MCZ, ANSP); Awaji-shima (Island) (USNM, MCZ); Wakanura; Takami (both USNM). KYUSHU: Nagasaki; Camp Mower, Sasebo (both USNM); Hirado, Hizen (ANSP, USNM); Shimonoeki; Saigo, Doko Islands, Oki Group, Japan Sea, shore (both USNM). HOKKAIDO: Muroran (USNM); Hakodate (USNM, MCZ); Zenibako (BPM); Otaru; Kamoiito, Teshio (both USNM).

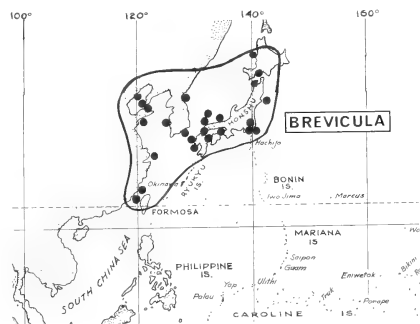


Plate 331. Geographical distribution of *Littorina breviculus* (Philippi.)

Subgenus *Littoraria* Griffith and Pidgeon, 1834Type: *Littorina zebra* (Donovan, 1825)

Members of this subgenus are inhabitants of tropical and subtropical portions of the Indo-Pacific, East Pacific and West Atlantic, but representatives appear to be absent from the East Atlantic. Although the type-species of *Littoraria* is from tropical west America, the majority of species live in the Indo-Pacific with one species in the Caribbean area. This may reflect what appears to be a trend toward a higher rate of speciation in the Indo-Pacific. In this group the

species generally are of medium size and are moderately robust; they are usually marked with axial or zigzag color lines, or are of a distinct solid color. Apertural white lines, so common in certain species of *Littorina* s.s. and particularly of *Austrolittorina*, *Nodilittorina* and *Granulilittorina* are usually absent or diffuse in *Littoraria*. All species probably produce a pelagic egg capsule, although observations on reproductive habits have been made on only a few. Possible evidence of a common lineage is given by the presence in most species of a basal flap on the penis; the flap contains no penial glands or "klebdrusën" as it does in other littorines.

Synonymy—

1834 *Littoraria* Griffith, and Pidgeon, The Animal Kingdom, vol. 12, Mollusca and Radiata, Index, p. 598, pl. 1, fig 3. Type-species by monotypy: *Littoraria pulchra* 'Gray' (Sowerby, 1832) [= *Littorina zebra* (Donovan, 1825)].

Key To Principle Recent Species of Indo-Pacific *Littoraria*

1. Shell variously color patterned 2
1. Shell without color pattern, plain pinkish gray *coccinea* p. 05-301
2. Columella generally blue to violet 3
2. Columella white 4
- 3a. Color pattern of brown undulate flammules or spots *undulata* p. 05-298
- 3b. Color pattern diffuse, whorls encircled with faint gray band ... *mauritiana* p. 05-304
- 3c. Color pattern of rather straight, closely-spaced brown axial lines ... *kraussi* p. 05-306
4. Color pattern a "herring-bone" effect, spire less than half the length of shell, white apertural band present *practermissa* p. 05-307
4. Color pattern of closely-spaced brown punctations, spire more than half the length of shell, no white apertural band *pintado* p. 05-297

***Littorina undulata* Gray, 1839**

(Pls. 325, 332, 333)

Range—From Madagascar to western Polynesia; apparently rare in Hawaii; not reported from southeastern Polynesia nor from east Africa.

Remarks—Due to its variability some forms of *Littorina undulata* are rather easily confused with several other Indo-Pacific species: *L. scabra* and *L. coccinea*, *L. mauritiana* and *L. kraussi*. From *L. scabra* it differs markedly in the anatomy of external reproductive structures, a large penile basal flap being present in *undulata*, whereas in *scabra* the entire base of the penis is thickened; *scabra* reproduces ovoviviparously while *undulata* produces a pelagic egg capsule; *scabra* usually inhabits mangroves and other wooden structures such as pilings, but *undulata* is usually

found on rocks; the shell of *undulata* is smaller (24 mm.) at maturity than *scabra* (over 40 mm.); although color patterns may appear superficially similar, upon close examination it may be noted that in *scabra* axial color markings are applied in a mosaic, the interruptions caused by the deeply incised spiral sculpture, while in *undulata* the markings appear continuous.

The relationship is closer between *undulata* and the three other species, *coccinea*, *kraussi* and *mauritiana*. The features of all four are somewhat similar, and indeed they are considered members of the same subgenus, *Littoraria*. In the case of these species differences from *undulata* are more subtle and involve character of and presence or absence of color pattern, sculptural differences, relative proportions and geographical ranges (see species descriptions).

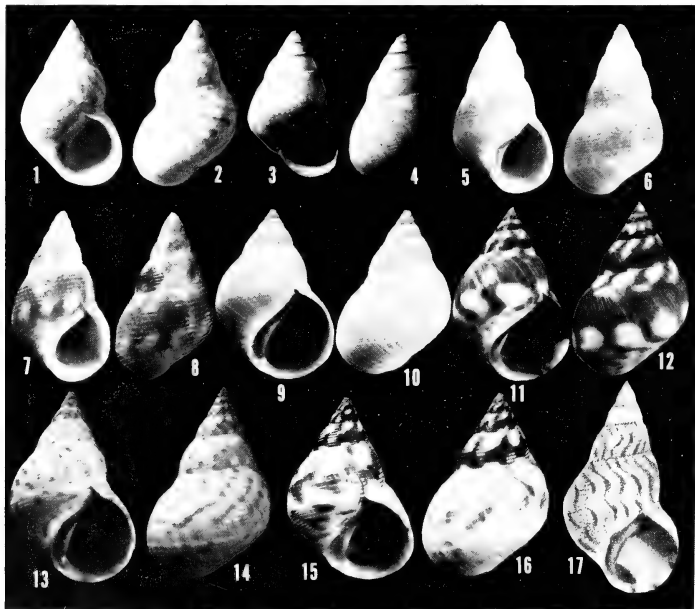


Plate 332. *Littorina (Littoraria) undulata* (Gray).

Figs. 1,2. Lectotype of *L. undulata* (BM(NH) 1968362; 22.8 × 12.6 mm.).

Figs. 3,4. Lectotype of *L. tenuis* Philippi from Ticao Island, Philippines (BM(NH) 1968276; 14.7 × 8.4 mm.).

Figs. 5,6,7,8. *L. acuminata* Gould from Mangsi Island [Philippines] (figs. 5,6: Holotype, USNM 5638; 8.9 × 4.8 mm.; figs. 7,8: paratype, USNM 612325, 6.8 × 3.7 mm.).

Figs. 9-16. *L. undulata* from various localities: figs. 9,10.

Pulau Stupai, Mentawai Ids., S.W. Sumatra (USNM 655218; 17.8 × 10.8 mm.); figs. 11,12. Pulau Siburu, N. of Sipora, Mentawai Ids., S.W. Sumatra (USNM 654710; 12.2 × 7.3 mm.); figs. 13,14. Bikini, Marshall Islands (USNM 585104; 20.05 × 11.8 mm.); figs. 15,16. Hienghene, New Caledonia (USNM 666080; 17.3 × 10.05 mm.).

Fig. 17. Lectotype figure of *L. columna* 'Jonas' Philippi, from *Abbildungen und Beschreibungen Conchylien*, vol. 3, pl. 6, fig. 15 (about 18 × 11 mm.).

The western Atlantic *Littorina nebulosa* (Lamarck) is the analogue of the Pacific *L. undulata*.

Habitat—Lives intertidally on rocky shores and commonly clusters in rock crevices during daylight hours, becoming active at night and crawling about on the rocks. Often associated with *L. coccinea* (Gmelin) where their ranges overlap.

Description—Shell reaching 23.9 mm. (about .9 inch) in length, turbinate in shape, average obesity about .58 (24 specimens range from .50 to .64) moderately thick in structure, imperforate, and sculptured with spirally incised lines, overall microscopic wavy spiral threads and fine, but rather regular oblique axial lines of growth. External color very variable: from a mottled yellowish gray to banded dark-brown, most often with continuous to interrupted undulating brown color markings; spire whorls often with white flammules on upper half, solid brown below; aperture light yellowish brown to dark yellowish brown sometimes with outside color markings showing through; columella usually grayish violet but sometimes lacking this color and being white, edged with brown. Base not flattened, separated from upper part of body whorl by a weak keel at periphery. Whorls 5-9, usually rather well rounded. Spire less than half the length of shell, convex, produced at an angle of about 58°. Aperture broadly oval; outer lip thin in young individuals to moderately thick in adults; inner lip strongly produced, hardly concave, oblique, glazed with a grayish violet callus, pinched where it joins outer lip at base of columella. Suture impressed. Sculpture consisting of from 7-10 spiral striae on spire whorls, persisting on entire surface of body whorl where as many as 16 may be present above weak keel, and about the same number below; on body whorl somewhat weaker secondary striae may occur between primary ones especially at suture and near periphery. Entire surface covered with microscopic, closely-spaced wavy spiral threads not easily detectable in worn specimens. Axial sculpture consisting of rather regularly-spaced, oblique growth lines which upon crossing spiral sculpture produce a weak reticulation. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decollate in all specimens examined; remaining portions smooth and glassy; first 2-3 post-nuclear whorls light-brown and sculptured with spiral striae. Radula typically littorinid (2-1-1-1-2).

Animal darkly pigmented on upper surface of tentacles, snout and foot. Verge with a large flap at its base, long and slender, but constricted about half its length and with a delicate translucent distal extremity. Seminal duct deeply folded. Reproduction oviparous; egg capsules observed to contain single ovum; capsule simple, convexo-convex, with flotation "skirt." Capsule diameter ranging from .23-.25 mm., ovum diameter .09-.11 mm. Development undoubtedly pelagic; well-developed veligers remaining in capsules on fifth day (Eniwetok-February) after shedding of capsule; pelagic stage probably long lived.

Measurements (mm)—			locality
length	width	no. whorls	
23.9	11.9	8+	Pulau Nias, S.W. Sumatra
21.8	12.0	6+	Guadalcanal, Solomon Islands
19.8	10.6	6+	Guadalcanal, Solomon Islands
19.7	11.6	6+	S.W. tip Sanding Id., Mentawai Ids.
18.0	10.3	6+	Guadalcanal, Solomon Islands
17.4	11.1	5+	Bikini Atoll, Marshall Islands
15.7	9.9	6+	Bikini Atoll, Marshall Islands
14.5	7.8	7+	Pulau Nias, S.W. Sumatra
11.3	6.5	8	Pulau Nias, S.W. Sumatra
10.9	6.1	8	Pulau Nias, S.W. Sumatra

Synonymy—

1839 *Littorina undulata* Gray, The Zoology of Captain Beechey's Voyage—in His Majesty's Ship *Blossom*, *Mollusks*, p. 140 (no locality given; not figured); type locality here designated: Okinawa, Ryukyu Islands; Lectotype BM(NH) 1968362, British Museum (N.H.).

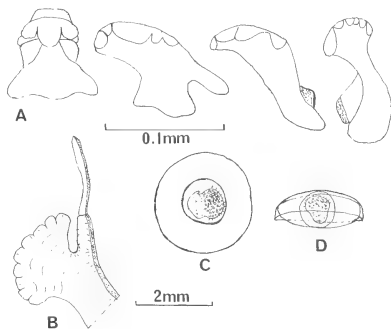


Plate 333. *Littorina (Littoraria) undulata* (Gray)

Fig. A. Radula (upper scale is 0.1 mm.).

Fig. B. Penis (lower scale is 2 mm.).

Fig. C. Egg capsule from above.

Fig. D. Egg capsule from side to show flotation "skirt" (capsule diameter about 0.23 mm.); all from Eniwetok, Marshall Islands.

- 1846 *Littorina tenuis* Philippi, Proceedings of the Zoological Society of London (1845) p. 141 (Ticao Island, Philippines); 1847 *Abbildungen und Beschreibungen* Conchylien, vol. 3, p. 18, pl. 6, fig. 8; lectotype and two paralectotypes, British Museum (N.H.) 1968276
- 1847 *Littorina columna* Jonas' Philippi, *Abbildungen und Beschreibungen* Conchylien, vol. 3, p. 14, *Littorina* pl. 6, fig. 15 (no locality given).
- 1849 *Littorina acuminata* Gould, Proceedings of the Boston Society of Natural History, vol. 3, p. 84 (Mangsi [Mangsee] Id. [Balabac Strait, Philippines]); 1852, U.S. Exploring Expedition, Vol. 12, p. 200, pl. 14, fig. 239 a, b, Holotype: USNM 5638.
- 1878 *Littorina scabra concolor* Weinkauff, *Systematisches Conchylien-Cabinet*, vol. 2, part 9, p. 37, pl. 4, fig. 11 [indicated in text]; in part (figs 8-10 are *L. scabra*) (Indo-Pacific).
- 1885 *Littorina undulata contracta* Nevill, *Hand List of Mollusca in the Indian Museum, Calcutta*, part 2, p. 143 (Andamans).
- 1885 *Littorina undulata sulcatula* Nevill, *ibid.*, p. 144 (Ascension Island, Pacific [Ponape, Caroline Ids.]; refers to Reeve, 1857, *Conchologia Iconica*, vol. 10, *Littorina*, pl. 13, fig. 67a [occasional specimens approach this degree of rugosity]).
- 1885 *Littorina conica subintermedia* Nevill, *ibid.*, p. 150 (Port Canning and False Point [Bengal, India]).

Types—From the 3 syntypes of *L. undulata* in the British Museum (NH), catalogue number BM(NH) 1968362, the one most closely approximating Gray's measurements and description is here designated as lectotype (length 22.8, width 12.6 mm.; see our pl. 332 figs. 1, 2). Gray listed no type locality, but there are few places where the *Blossom* touched land within the range of this species (see Beechey, 1831; Rosewater, 1968). One such place, Okinawa, Ryukyu Islands, is here designated as the type locality. The specimen of *L. tenuis* Philippi BM(NH) 1968276, figured in *Abbildungen und Beschreibungen*

Conchylien pl. 6, fig 8, is here designated lectotype (14.7 x 8.4 mm.; see our pl. 332 figs. 3, 4). The type specimen of *L. columna* Philippi may be in the Berlin Museum. The types of *L. contracta*, *subintermedia* and *sulcatula* Nevill should be in the Indian Museum, Calcutta. The holotype of *L. acuminata* Gould is in the U.S. National Museum (USNM 5638). The location of the type of *L. concolor* Weinkauff is unknown to me.

Records—MADAGASCAR: Ambodifototra, Ile Ste. Marie; Ile aux Nattes, S. of Ile Ste. Marie; Faty, 13 mi. N. of Tulear (all MCZ); MAURITIUS: Pt. d'Espy N.E. of Poste de Flacq; E. of Souillac on Savanne River (both ANSP); SEYCHELLES: Anse a la Mouche, Mahe Island (YPM); MALDIVES: South half Kendikolu Island, Miladummadulu Atoll; btwn. Mahleluri and Maro Islands, Fadifolu Atoll; Dunidu Island, N. of Male, North Male Atoll; Ari Atoll (all USNM, ANSP); Hitadu Id., Haddumati Atoll (YPM); Wala Island, South Nilandu Atoll; N.W. tip of Gan, Addu Atoll (both ANSP).

INDIA: Vengurla, N. of Goa; Khumta (Kumta), N. Kanara (all USNM); Cochin, Malabar (MCZ, AMS); Cape Comorin; Remen Point, west side Pamban Pass, btwn. Gulf of Mannar and Palk Strait (both ANSP, USNM); Mandapam Camp (USNM); Madras (ANSP, MCZ). CEYLON: shore, Ft. Frederick, Trincomalee (ANSP, YPM); Weligama Bay; Pointe de Galle; Galle (all ANSP); Colombo (USNM, MCZ, NMW, SMF); Delft Island; Kankasanturai; W. of Kankasanturai; Merissa Village (all ANSP). MALAYSIA: Pulau Anyut, Malacca Strait, just S.W. of town of Malacca (USNM). THAILAND: Goh Huyong, Similan Islands; Goh Phi Phi (both USNM). FORMOSA: (ANSP). JAPAN: Higo (Higo Shima) (USNM); Hachijo Island, 275 mi. S. of Tokyo, Honshu (ANSP); Kagoshima (USNM); Oshima, Osumi (USNM, MCZ). RYUKYU ISLANDS: Okinoerabu-shima (ANSP); 1 mi. N. of Shana Wan, Okinawa Island (USNM); Nago, Okinawa Island (BPBM, MCZ); Awa (ANSP). PHILIPPINES: Many localities, including the following islands: Batanes; Babuyan; Luzon; Burias; Mindoro; Panay; Cebu; Bohol; Mindanao; Basilan; Palawan (all USNM). SULU ARCHIPELAGO: Jolo Island; Simaluc Island, Tataan Islands, Tawi Tawi Group; Marongas Island, Jolo (all USNM). BORNEO: Sipitang; West Marudu Bay; Taganak (all USNM). CELEBES: Macassar (MCZ). MOLUCCAS: Karakelong Island, Talaud Islands (MCZ); Morotai, Halmahera Group, (USNM); Kasiroeta Is-

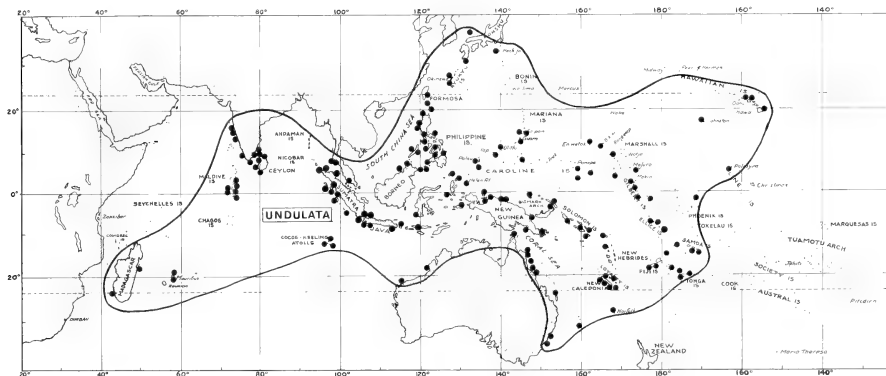


Plate 334. Geographical distribution of *Littorina* (*Littoraria*) *undulata* (Gray).

land; Salangadeke Island, N. Loloda, W. of Halmahera Island (both MCZ); Ceram (USNM); Hajar, Manipa Island (MCZ). SUMATRA: Pulau Melila, S. of Udjung Batu, Bank Islands (USNM); Pulau We (MCZ, ZMA); Pulau Boenta, off Aceh Head; Pulau Nias (both USNM); Padang (MCZ); Pulau Siburu, N. of Sipora; Veeckens Bay, South Pagi Island; Pulau Stupai, north edge Sanding Island, Mentawai Islands; south-west tip of Sanding Island, Mentawai Islands (all USNM); Marong (ANSP). JAVA: Pelabuhan Ratu, Praeger (MCZ, USNM); Welkomst Bay, Banten (USNM); Pemeungpeuk, nr. Garut, S.E. coast of Java (MCZ). BALI (AMS). FLORES ID. (ZMA). COCOS KEELING: North Keeling, near Pulo Selwa; Cocos Lagoon; "Coral Pits," Klapa Tuju, West Island (all USNM).

WESTERN AUSTRALIA: Broome; Ridell's Beach, 2 mi. S.E. of Gantheaume Point, Broome; Gantheaume Point, Broome (all ANSP); S. end South Pasco Island, Barrow Island Group, off Onslow (WAM, USNM). NEW SOUTH WALES: nr. Wollongong (USNM); Port Stephens (AMS). QUEENSLAND: Heron Island, Capricorn Group (AMS); Cape Cleveland, nr. Townsville (USNM); Palm Island (AMS); Brook Island (ANSP); Flying Fish Point; Russell River; Fitzroy Island; nr. Cairns; Lizard Island (all AMS); Green Island, nr. Cairns (MCZ); Cooktown; Murray Id., Torres Strait (both AMS). NEW GUINEA: Hollandia; Aitape; outlet of Kalveng River, Gusika, 13 mi. N. of Finschhafen (all MCZ); Huon Gulf (USNM); Collingwood Bay (AMS); Yule Island (USNM); BPBM; ANSP; MCZ); Island 1/2 mi. S.W. of Sowe, Soepiori, Schouten Islands (MCZ); Biak; N.E. end of Noekori Island; N. Noesi Isle, Mios Woendi Atoll, Padoia Islands; Rainbawi Point, Japan Island; S.E. entrance to Woori Bay, Japan Island; Montoewoeri Point, Koeroedoe Island; Abroeki Island, Maransabodi Island, Aeri Islands, Geelink Bay (all ANSP). ADMIRALTY IDS.: Koruniat Island (ANSP). BISMARCKS: New Ireland (MCZ, USNM); Matupi Island, Rabaul, New Britain (AMS). SOLOMONS: Woodlark Island (USNM); Harapa, Shortland Island (MCZ); nr. mouth of Langa River, N. shore Guadalcanal (MCZ, ANSP); Point Purvis, Florida Island; Ugi Island (both USNM); Makira Harbor, San Cristobal (AMS). SANTA CRUZ IDS.: Tinakula (AMS). NEW HEBRIDES: Pakea, Banks Group (AMS). LOYALTIES: Lifou (USNM, AMS); Maré (MCZ). NEW CALEDONIA: N. of Hienghene (AMS); Koe Reef, 2 mi. S.E. Touho (ANSP); Isle of Pines (MCZ); Ilot Maitre, about 4 mi. S.W. of Noumea; (ANSP); Ilot Amédée (AMS); La Roche, Bourail; Gatope Island, Voh (both ANSP). LORD HOWE ISLAND: Norfolk Island (both AMS). FIJI: Point N. of Namu, NNE Viti Levu (MCZ); Irvines, nr. Malaqeregere, S.W. Viti Levu (USNM); Lakemba (BPBM). MARIANAS: Saipan (ANSP; USNM; NMW); Tinian (MCZ); Tumon Bay, Guam (BPBM). PALAUS: Koror, Malakal Dock; Eil Malk (both ANSP); Angaur (BPBM, MCZ). HELEN REEF: N. end Helen Islands (ANSP). CAROLINE ISLANDS: Tomil Harbor Yap Island (USNM); Ulithi Atoll (ANSP); Elato Atoll (USNM); Dublon, Truk; Ponape (both BPBM); Kusaie (AMS, BPBM, MCZ); Kapingamarangi (USNM). MARSHALL ISLANDS: Eniwetok; Bikini; Kwajalein; Arno; Jaluit; Ebon Atoll (ALL USNM).

GILBERTS: Abaiang (MCZ); Maiana; Tabiteuea (both BPBM). HAWAIIAN ISLANDS: Kailua, Oahu (BPBM); Kamilo, Kau; Keaukaha, Hilo, both Hawaii (both USNM). LINE ISLANDS: Palmyra (USNM). JOHNSTON ISLAND (USNM, BPBM). ELLICE ISLANDS: Nui; Vaitupu; Nukualailai (all USNM). WALLIS ISLANDS: Nukuhifala; btwn. Luanna and Fungalei Islands (both USNM). HOORN ISLANDS: Futuna (USNM). PHOENIX ISLANDS: Canton Island (USNM). SAMOA: Salelei Village, Upolu Island (ANSP); Pago Pago, Tutuila (BPBM; USNM). TONGA: Niuafu Island; Niutoua, Tongatapu; Laulea Reef, nr. Fatuma, Tongatapu (all USNM); Velitoo; Tongatapu; Nomuka, Ha'apai (both BPBM).

Littorina coccinea (Gmelin, 1791)

(Pls. 325, 335, 336)

Range—Cocos-Keeling Islands to Eastern Polynesia, including Hawaii.

Remarks—The name *coccinea* is derived from the Latin "coccineus" meaning "red like a berry" and seems to be a misnomer in the case of adult specimens which are largely whitish. There is, however, always a blush of brownish orange coloration which shows through and the aperture is intensely colored. Young individuals show more of the color which perhaps prompted Gmelin to adopt Martyn's appellation and, in addition, Martyn's plate shows an exaggeratedly red-colored individual. Although evidencing no outstanding characteristics the species is easily recognizable and in the center of its range, Micronesia, probably is the most common littorinid present (see Demond, 1957).

Habitat—Lives intertidally on rocky shores and commonly clusters in rock crevices during daylight hours, becoming active at night and crawling about on the rocks. Often associated with *L. undulata* Gray where their ranges overlap.

Description—Shell reaching 25.8 mm. (slightly over 1 inch) in length, elongate- to conic-

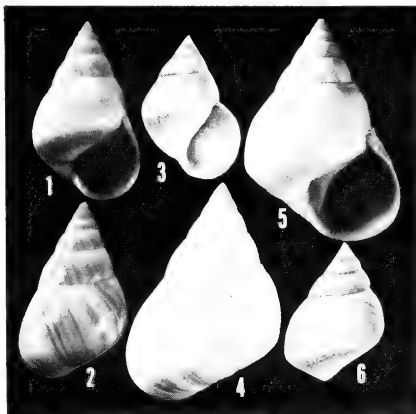


Plate 335. *Littorina (Littoraria) coccinea* (Gmelin).

Figs. 1,2. Specimen from Aitutaki, Cook Islands, showing diffuse color-banding (USNM 684817; 14.3 × 8.1 mm.).

Figs. 3,6. Lectotype figure, from T. Martyn, Universal Conchologist, vol. 2, pl. 68 [external figs].

Figs. 4,5. Specimen from Vitilevu, Fiji, nearly white with little evidence of external color or banding (USNM 531795; 22.7 × 14.0 mm.).

turbinate in shape, average obesity about .60, 21 specimens ranging from .56-.65, females slightly more obese than males), older individuals relatively thick in structure, imperforate, and sculptured with spirally incised lines, overall microscopic, wavy, spiral threads and irregular, oblique lines of growth. External color white, lacking patterned color markings except for occasional circular white blotches on early whorls; with brownish orange to strong brown within the aperture and showing through on lower portions of early whorls, on center of body whorl and on the base of shell. Base only slightly flattened, separated from upper part of body whorl by a weak to moderate keel at the periphery. Whorls 6-9, moderately rounded. Spire less than half the length of shell, convex, produced at an angle of about 60°. Aperture roundly oval; outer lip thin in young individuals to moderately thick in adults; inner lip concave, curves obliquely posteriorly, glazed with the brownish orange callus, pinched where it joins outer lip at base of columella. Suture distinctly impressed.

Sculpture consisting of from 7-10 spiral striae over entire surface of early spire whorls, but often becoming indistinct on penultimate and body whorls where the first 1-5 striae only may be visible; first subsutural stria the strongest, producing a shouldered effect. Entire surface of shell covered with microscopic, closely-spaced wavy spiral threads not easily detectable in worn speci-

mens. Axial sculpture consisting of occasionally coarse but usually fine oblique lines of growth. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decollate in all specimens examined; remaining portions smooth and glassy; first 2-3 post-nuclear whorls brownish orange and sculptured with spiral striae. Radula typically littorinid (2-1-1-1-2).

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verge long and slender, with a swollen enlargement at its base. Reproduction oviparous; pelagic egg capsules observed to contain single ovum; capsule simple, convexo-convex, with flotation "skirt." Capsule diameter 0.24; ovum diameter .09 mm. Development undoubtedly pelagic; veliger stage reached in 2-3 days (Eniwetok-February) after shedding of capsules; some larvae swimming free at that time.

Measurements (mm)—

length	width	no. whorls	locality
25.8	15.0	6+	Keaukaha, Hilo, Hawaii
23.0	14.3	5+	Bikini Atoll, Marshall Ids.
20.4	12.0	9	Futuna, Hoorn Ids.
18.1	10.5	8+	Makatea, Tuamotu Ids.
15.3	9.2	8+	Makatea, Tuamotu Ids.
14.3	9.3	9	Makatea, Tuamotu Ids.
12.7	7.4	7	Huahine, Society Ids.
11.2	6.3	8+	Moorea, Society Ids.
9.8	5.8	7	Moorea, Society Ids.
7.2	4.2	6+	Moorea, Society Ids.

Synonymy—

- [1788 *Limax coccinea* Martyn, Universal Conchologist, Vol. 2, plate 68; rejected work, non-binomial.]
- 1791 *Helix coccinea* Gmelin, Systema Naturae, edition 13, vol. 1, part 6, page 3651 (New Zealand [Tahiti, Society Islands, here corrected]); refers to Martyn, Univ. Conch. 2, t. 68, f. ext [restricted to external figures; the figure on left (apertural view) here designated as lectotype].
- 1832 *Littorina obesa* Sowerby, Genera of Recent and Fossil Shells, vol. 32, no. 37, fig. 6 [fig 6 here designated as lectotype] (South Sea Islands)
- 1839 *Littorina limax* Gray, The Zoology of Captain Beechey's Voyage in His Majesty's Ship Blossom p. 139 (Society Islands); refers to Martyn, Univ. Conch. [vol. 2, pl. 68, left external figure here designated as lectotype].

Types—Gmelin based the name *Helix coccinea* on the figures in Martyn's Universal Conchologist (vol. 2, pl. 68, external figures). The location of Martyn's collection is not known and therefore we must resort to his figures to distinguish this fortunately distinctive species. The left hand figure, apertural view, is here designated as lectotype of Gmelin's *Helix coccinea*. The type locality, given by Gmelin as New Zealand is here corrected to Tahiti, Society Islands, a likely place

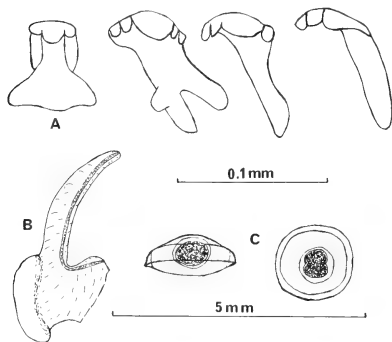


Plate 336. *Littorina* (*Littoraria*) *coccinea* (Gmelin), from Eniwetok, Marshall Islands.

Fig. A. Radula (upper scale = 0.1 mm.)

Fig. B. Penis (lower scale is 5 mm.)

Fig. C. Two views of egg capsule (diameter of capsule about 0.24 mm.; diameter of egg about 0.09 mm.).

for Martyn's figured specimen to have been collected.

The location of type specimens of *L. obesa* Sowerby and of *L. limax* Gray are also unknown; they were not found in the collection of the British Museum (N.H.) during a recent visit there (1968). For *L. obesa*, Sowerby's figure 6 is here designated as lectotype; for *L. limax*, Martyn's left external figure, pl. 68 of the Universal Conchologist, vol. 2, is here designated as lectotype.

Records—FORMOSA (ANSP). RYUKYU ISLANDS: Kikai-shima; Okinawa (both USNM). PHILIPPINES: Sabtan Island; Santo Domingo, Batan Island, both Batanes Group; Cujangan Island; Candaraman Island, Balabac (all USNM). INDONESIA: Karakelong Island, Moluccas (MCZ). COCOS-KEELING ISLANDS: North Keeling (USNM). AUSTRALIA: Murray Island, Torres Strait; Lizard Island, (both AMS); Green Island, nr. Cairns (MCZ); Herald Cays, off Cairns; West Cay, Diamond Islets; Russell Island; Flying Fish Point, all Queensland (all AMS). NEW GUINEA: 5 mi. N.W. of Rani Island, Biak Island, Schouten Islands, (ANSP); Hollandia (MCZ). BISMARCKS: Malie Island, Lihir Islands, New Ireland (AMS). SOLOMONS: Stirling Isle, Treasury Islands (USNM); Simbo Island (AMS, ANSP); Ugi Island (USNM); Morlock Ids. (Del. Mus. Nat. Hist.). SANTA CRUZ ISLANDS: Vanikoro (AMS). NEW HEBRIDES: Espiritu Santo Island (MCZ); Vate Island (Elate Island) (AMS); Tana Island (USNM). LOYALTIES: Uvea Island (USNM); Lifou Island (AMS). NEW CALEDONIA: N. of Touho (ANSP, USNM); Ilot Maitre S.W. of Noumea (ANSP). LORD HOWE ISLAND (AMS); FIJI: Cebu Island, Nandronga; Irvines, Nr. Malaqeregere, both Viti Levu; Fulanga, Lau Group (all USNM). MARIANAS: Saipan Island (ANSP, MCZ); Tinian (USNM, MCZ); Tumon Bay, Guam (BPBM); Apra Bay, Guam (USNM). PALAUS: S.E. Eil Malk; S.E. Aulupatagel Island, Malakal Harbor, Koror (both ANSP). CAROLINES: Yap (BPBM); Mog Mog Ulithi (BPBM, USNM); Ponape (MCZ); Kusaie, "Coral Islet" Lele (BPBM); Kapingamarangi (USNM,

BPBM). MARSHALL ISLANDS (many localities on the following atolls): Eniwetok; Bikini; Rongelap; Rongerik; Ujae; Pokak; Bikar; Taka; Uterik; Wotho; Likiep; Ailuk; Arno; Lae; Kwajalein; Ailinglapalap; Jaluit Atoll (all USNM). GILBERTS: Abaiaing Island (MCZ); Abemama Island (USNM); Tabiteuea (BPBM). HAWAIIAN ISLANDS: Kaaawa, (USNM); Koko Head, western side, both Oahu (BPBM); Hilo, (MCZ, USNM); Kapoho, (BPBM); Pohoiki, all Hawaii (USNM).

LINE ISLANDS: Kingman Reef (BPBM); Palmyra Island (ANSP, USNM, AMS, MCZ, BPBM); Washington Island (BPBM); Fanning Island (BPBM, AMS); Flint Island (USNM, ANSP). JOHNSTON ISLAND (USNM, MCZ, BPBM). EL LICE ISLANDS: Nanumea; Nui (both USNM); Funafuti (AMS, MCZ, USNM); Nukulailai (USNM); Rotuma (BMNH). WALLIS ISLAND: Nukuhifala (USNM). HOORN ISLANDS: Futuna (USNM). HOWLAND ISLAND (BPBM). BAKER ISLAND (BPBM). PHOENIX ISLANDS: Canton Island (USNM). SAMOA: Apia (USNM, AMS); Saluafata reefs, both Upolu (ANSP); Pago Pago Harbor, (BPBM, USNM); Anuu Island, both Tutuila (MCZ); Ta'u Island (BPBM, MCZ); Fakaofa Island (BPBM), Tokelau Ids. TONGA: Niuafo'ou (USNM, BPBM); Lifuka, Ha'apai Group; Velitua, (both BPBM); Popua Reef, Tongatapu (USNM). COOK ISLANDS: North tip Aitutaki, Aitutaki (USNM); Taungani, Mauke (BPBM); Rarotonga (AMS); Avatiu Harbor to Motu Tou, Rarotonga; Mangaia (both USNM, MCZ). AUSTRAL ISLANDS: Raeivavae, (USNM). SOCIETY ISLANDS: Fanui Bay; S. of Farepiti Point; Vaitape Village all Bora Bora; around point from "Hipu"; Bay Vaoire both Tahaa; Uturoa; Ilot Tipaemanu S.E. of Uturoa; Tevaitoa, all Raiatea; Point Teffaoa, around reef, Huahine; Moto Fareone; Opunohu Bay (all USNM); Pareau Point, District of Teavaro (ANSP), all Moorea; Tiare; btwn, Hanuta River and Fautaua River, Pirae; Patutoa (all USNM); Atue, Punaauia (ANSP); 43 km. N. of Pariatua, Hitiaia, (USNM); btwn. mouths of Maruapo and Hapaa Rivers, District of Punaauia (ANSP); 1 km. S. of Faone River, Faone; Motu Fenuaina, Tautira (both USNM) all Tahiti. TUAMOTUS: Tikehau; Vahitahi; Reao; Tureia; Makemo (all USNM); Takaroa; Niau; Toao; Amanu (all ANSP); Makatea; Fakarava; Raroia (all ANSP, USNM). GAMBIER ISLANDS: Mangareva (MCZ; USNM; AMS). Oeno Island; Pitcairn Island (both USNM). HENDERSON ISLAND (Smith, 1913).

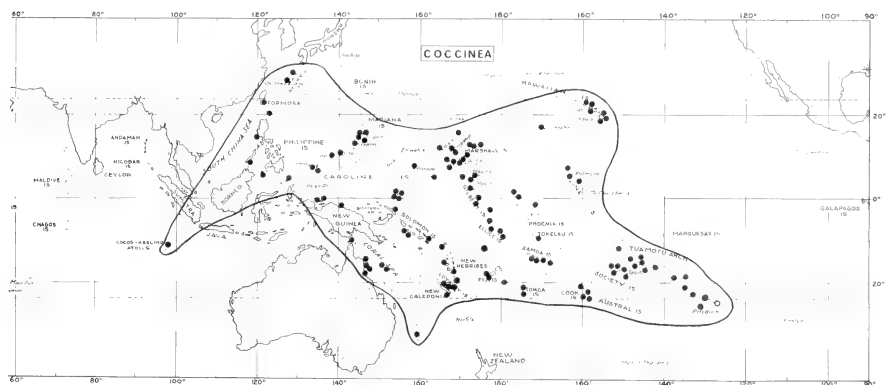


Plate 337. Geographical distribution of *Littorina* (*Littoraria*) *coccinea* (Gmelin).

***Littorina mauritiana* (Lamarck, 1822)**

(Pls. 325, 338, 339)

Range—South Africa and Southwestern Indian Ocean Islands.

Remarks—*Littorina mauritiana* is restricted in its distribution to the southwestern Indian Ocean. It has been confused quite often with similar appearing species from South Africa, Australia and New Zealand but is unquestionably distinct when its peculiarly smooth gray banded shell and diffuse markings are recognized. The species most commonly confused with *L. mauritiana* is *L. unifasciata* and its subspecies in Australia, New Zealand and Juan Fernandez, but it is easily distinguished on the basis of shell and animal characters. This species is closely related to *Littorina coccinea* of the Western Pacific and also *L. kraussi* of the Indian Ocean.

Habitat—Intertidal on rocks.

Description—Shell reaching 24 mm. (about 0.9 inch) in length, turbinate in shape; average obesity about .59 (13 specimens range from .55 to .63), older individuals relatively thick in structure, imperforate; sculptured spirally with overall microscopic wavy threads and axially with occasional lines of growth. External color pattern rather constant, consisting of a spiral band of gray on middle of body whorl and on anterior third of spire whorls; area anterior and posterior to band with indistinct wavy axial color lines; anterior color lines ending at another rather indistinct gray spiral band on the base of body whorl with only occasional subsequent, sometimes obliquely spiral, color markings; overall background color a yellowish gray. Aperture usually dark brown, often with outside color pattern showing through; with an internal basal white spiral band and occasionally a small one posteriorly inside outer lip. Whorls 6-8 but spire often eroded. Spire less than half the length of shell, convex, produced at an angle of about 57° (but varying to as low as 48°). Aperture oval; outer lip thin in young specimens to moderately thick in adults; inner lip concave, curving obliquely posteriorly, glazed with a brown to violet callus, pinched where it joins outer lip at base of columella. Suture impressed. Sculpture consisting of microscopic, closely spaced, wavy spiral threads not easily detectable in worn specimens. Axial sculpture consisting of irregular lines of growth which may



Plate 338. *Littorina* (*Littoraria*) *mauritiana* (Lamarck)

Figs. 1,2. Lectotype of *P. mauritiana* from "Ile-de-France," (MHNG 1096/91-2, 22.8 × 13.2 mm.).

Figs. 3,4. Paralectotype (MHNG 1096/91-5, 12.5 × 7.4 mm.).

Figs. 5,6. Lectotype of *Littorina laevis* Philippi, (BM(NH) 1968221, 18.4 × 11.4 mm.).

Figs. 7,8. Holotype of *Tricolia citrea* Deshayes from Bourbon [Reunion] (MHNP, 6.1 × 4.2 mm.).

Figs. 9,10. *L. mauritiana* from Pointe Fayette, E. Mauritius, (USNM 637330 [ex ANSP 273712] 19.8 × 11.1 mm.).

Figs. 11,12. *L. mauritiana* from E. of Souillac, Mauritius, (USNM 637331 [ex ANSP 274078] 15.8 × 9.4 mm.).

(Figs. 1,2,7,8. R. Robertson photos; other photos by the author)

have associated dark pigmentation. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decoliate in all specimens examined; remaining portions smooth and unsculptured. Radula typically littorinid.

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verge moderately long and slender, with a terminally swollen branch near its base, similar to *L. kraussi*. Reproduction unknown; [probably oviparous and involving pelagic capsules].

Measurements (mm.)—

length	width	no. whorls	locality
24.0	13.3	7+	Mauritius
20.1	12.2	6+	Mauritius
19.9	11.1	8+	Mauritius
19.6	12.4	5+	Madagascar
18.9	10.8	5+	Mauritius
18.1	11.4	7+	Reunion
17.5	11.1	6+	Mauritius
17.4	9.8	6+	Mauritius
14.1	8.7	5+	Mauritius
11.4	7.0	6+	Mauritius

Synonymy—

- 1822 *Phasianella mauritiana* Lamarck, Histoire Naturelle des Animaux sans Vertèbres, vol. 7, p. 54 (Ile-de-France [Mauritius]); Lectotype in Muséum d'Histoire Naturelle, Geneva MHNG 1096/91-2, 22.8 x 13.2 mm.
- 1838 *Phasianella mauritiana* Lamarck Potiez and Michaud, Galerie des Mollusques, Muséum de Douai, vol. 1, p. 311 (error for *P. mauritiana* Lamarck, 1822).
- 1846 *Littorina laevis* Philippi, Proceedings of the Zoological Society of London (1845), part 13, p. 140 (locality unknown [Mauritius here selected]); Lectotype in British Museum (N.H.); BM(NH) 1968221, 18.4 x 11.4 mm. 1847, Abbildungen und Beschreibungen Conchylien, vol. 3, p. 10, *Littorina*, pl. 6, fig. 6.
- 1847 *Littorina mauritiana gracilior* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 165, *Littorina*, pl. 3, fig. 17b [right hand fig.]. Probably is eastern Pacific species best known as *L. modesta paysonensis* Philippi, 1847.
- 1863 *Phasianella vitrea* Deshayes, Catalogue des Mollusques de L' Ile de la Reunion, (Bourbon) p. 76, pl. 8, fig. 8 (Bourbon); Holotype in Muséum d'Histoire Naturelle, Paris, 6.1 x 4.2 mm.).

Types—There are 5 syntypes of *Phasianella mauritiana* in the Lamarck Collection of the

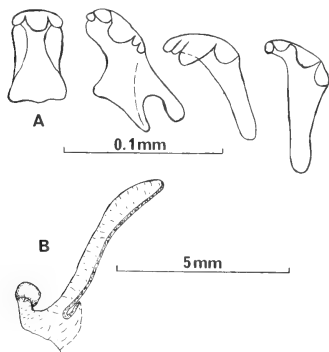


Plate 339. *Littorina (Littoraria) mauritiana* (Lamarck) from Pointe Fayette, E. Mauritius (ANSP 273712)

Fig. A. Radula (upper scale is 0.1 mm.)

Fig. B. Penis (lower scale is 5 mm.)

Muséum d'Histoire Naturelle, Geneva, representing three different species of Indo-Pacific Littorinidae: *L. mauritiana*, *L. kraussi*, and *L. unifasciata*. The last cannot have occurred at Mauritius, which Lamarck clearly stated as type locality, and *L. kraussi* does not fulfill both requirements of Lamarck's description: shell "bluish white" and columella "violet blue." Syntypes 2 and 5 (MHNG 1096/91-2, 5) do fulfill these requirements and are here designated as Lectotype and paralectotype respectively of *Phasianella mauritiana* Lamarck (see our pl. 338, figs. 1-4)

The specimen of *L. laevis* which Philippi figured in Abbildungen und Beschreibungen Conchylien vol. 3, pl. 6, fig. 6, is in the British Museum (NH) BM(NH) 1968221, and is here selected as lectotype of that species (see our pl. 338, figs. 5, 6). The holotype of *P. vitrea* Deshayes is in the Muséum d'Histoire Naturelle, Paris (see our pl. 338, figs. 7, 8). The type specimen of *L. gracilior* Philippi may still be extant in the Berlin Museum.

Records—SOUTH AFRICA: Port Edward, Natal (ANSP). MADAGASCAR: Flacourt, Fort Dauphin (MCZ). SEYCHELLES: Praslin Island (Melville, 1909). MAURITIUS: S. side Tombeau Bay, W. Mauritius; E. Tamarin Bay, W. Mauritius; Pointe Fayette, E. Mauritius; E. of Souillac on Savanne River (all ANSP); Port Louis (MCZ). REUNION: Sainte Pierre (AMS). CHAGOS ARCHIPELAGO (Melville, 1909).

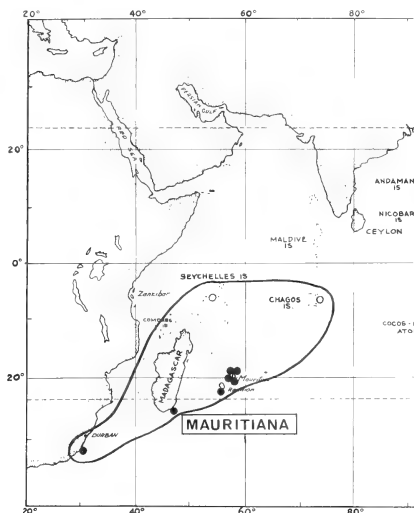


Plate 340. Geographical distribution of *Littorina (Littoraria) mauritiana* (Lamarck) in the southwestern Indian Ocean.

***Littorina kraussi* new name Rosewater, 1970**

(Pls. 325, 341)

Range—East coast of Africa, the Indian Ocean islands and south India to Cocos-Keeling Atolls.

Remarks—The familiar name *Littorina glabrata* Philippi, 1846, is unfortunately a secondary homonym of *Paludina glabrata* Pfeiffer, 1828 (= *Littorina neritoides* (Linné)), the Mediterranean species and, therefore, must be renamed. The species is renamed for F. Krauss from whom Philippi "stole" several South African species by publishing his manuscript names first. *Littorina kraussi* is closely related to *L. mauritiana*, *undulata* and *coccinea*.

Habitat—On rocks near high tide line.

Description—Shell reaching 21.8 mm. (about 0.9 inch) in length, turbinate in shape; average obesity about .58 (15 specimens range from .55 to .62); older individuals relatively thick in structure, imperforate, and sculptured with spirally incised lines, overall microscopic wavy spiral

threads and fine rather regular oblique axial lines of growth. External color pattern rather constant, consisting of moderately regularly spaced, oblique, zigzagging, or chevron-shaped brown markings superimposed on a lighter background; (pale to grayish-yellowish pink ISCC-NBS numbers 31-32) spire whorls above penultimate whorl often dark anteriorly and light posteriorly, particularly noticeable in small individuals; aperture light to darker brown, sometimes with exterior color markings showing through; columella variable in color; ranging from dark brown through violet to nearly white with a brownish tinge. Base not flattened, separated from upper part of body whorl by a weak to moderate keel at periphery. Whorls 6-7 or 8 but spire often eroded. Spire less than half the length of shell, convex, produced at an angle of about 55°. Aperture oval; outer lip thin in young specimens to moderately thick in adults; inner lip concave, curving obliquely posteriorly, glazed with a brown, violet or nearly white callus, pinched where it joins outer lip at base of columella. Suture impressed. Sculpture consisting of from 7-10 spiral striae on spire whorls and persisting onto body whorl where 10-11 may be present above the keel and about the same number below; striae evanescent in some specimens, worn away or weak at center of whorls. Entire

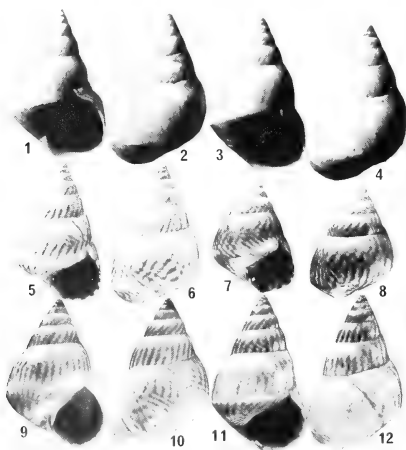


Plate 341. *Littorina (Littoraria) kraussi* Rosewater.

Figs. 1,2. Lectotype, *L. glabrata* [= *L. kraussi*] from Natal, South Africa (BM(NH) 1968220, 18.3 × 10.8 mm.).

Figs. 3,4. Paralectotype, same BM number, 18.4 × 11.1 mm.

Figs. 5,6. Tiladummati Atoll, Maldive Islands (USNM 672385, 17.7 × 10.5 mm.).

Figs. 7,8. The same, a smaller specimen showing more intense coloration (11.4 × 7.4 mm.).

Figs. 9,10. Zanzibar (USNM 89411, 14.7 × 8.9 mm.).

Figs. 11,12. Near Poste de Flacq, Mauritius (USNM 637326, 15.5 × 8.7 mm.).

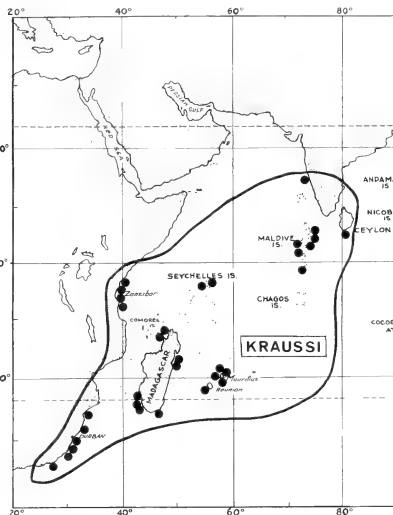


Plate 342. Geographical distribution of *Littorina (Littoraria) kraussi* Rosewater in the Indian Ocean.

surface covered with microscopic, closely spaced, wavy spiral threads not easily detectable in worn specimens. Axial sculpture consisting of rather regularly spaced lines of growth. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decolgate in all specimens examined; remaining portions smooth and glassy; first 1-2 post nuclear whorls light brown and usually sculptured with spiral striae. Radula typically littorinid and similar to *L. mauritiana*.

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verge long and slender with a terminally swollen branch near its base, appearing very similar to *L. mauritiana*. Reproduction unknown; [probably oviparous and involving pelagic capsules.]

Measurements (mm.)—

length	width	no. whorls	locality
21.8	11.9	6+	Mauritius
21.6	12.4	7+	Mauritius
19.8	11.6	7+	Mauritius
17.5	10.5	7+	Zanzibar
16.9	9.3	6+	Madagascar
14.4	8.6	7+	Mombasa, Kenya
13.1	7.5	6+	Madagascar
12.5	6.9	7+	Mombasa, Kenya
10.2	6.3	7+	Mombasa, Kenya
9.3	5.5	7	Madagascar

Synonymy—

1846 *Littorina glabrata* Philippi, Proceedings of the Zoological Society of London (1845) p. 140 (Payta Peru; and Cape Natal [South Africa] here restricted to second locality). 1848, *Abbildungen und Beschreibungen Conchylien*, Vol. 3, p. 62. *Littorina* pl. 7, fig. 5. Lectotype in BM (NH) 1968220; [Non *Paludina glabrata* Pfeiffer, 1828 = *Littorina neritoides* (Linnaeus, 1758)]. 1848, Krauss, Die Sudafrikanischen Mollusken, p. 103.

Types—Although it was necessary to supply a new name for the secondary homonym, *Littorina glabrata* Philippi, 1846, the type specimens are the same for both *L. glabrata* and *L. kraussi*. A lectotype is here designated from among the four syntypes of *L. glabrata* in the British Museum (NH) (BM (NH) 1968220, length 18.3, width 10.8 mm.; see our pl. 341, figs. 1, 2).

Records—SOUTH AFRICA: Miller's Point, False Bay (ZMA); Coffee Bay, 1 mi. S. Umata River; East London, at mouth Nahoon River; Second Beach, Port St. John; Port Edward; Margate, 11 miles south of Port Shepstone; Isipingo (all ANSP; NMW); Durban; mouth of Umhlali River (both MCZ). MOZAMBIQUE: Ilha da Inhaca, Delagoa Bay (ANSP). TANZANIA: Kendwa Island, 4 miles E.S.E. of Dar-es-Salaam (MCZ); Bungi, Kiwani Bay; Changa; E. side Puopo, Tumbat Island (all ANSP). KENYA: Mombasa Island (ANSP; NMW). ADEN: (RNHL; BM(NH); MHNP). MADAGASCAR: Anakao, 20.5 miles S. of Tulear; Soalany, 16 miles S. of Tulear; 1 mile N.W. of St. Augustin, 14 miles S.E. of Tulear; bay S. side Nosy Iranja, 32 miles S.W. of Nossi Bay;

Nosy Tany Kely, 4 miles S. of Nosy Be; Pte. Fievre, S. Nosy Be; S. of Anivorano, 12 miles N. of Ambodifototra, W. coast Ile Ste. Marie; Ambodifototra, Ile Ste. Marie; S.W. shore Ile aux Nattes S. of Ile Ste. Marie; Flacourt, Fort Dauphin (all R.W. Foster; ANSP; MCZ). SEYCHELLES: St. Pierre Islet; Mahé Island (both YPM); Praslin Id. (NMW). MAURITIUS: S.E. side Tamarin Bay; S. side Tombeau Bay; ¼ mile S.W. of Cape Malheureux; Pte. Lafayette; 1 mile N.E. of Poste de Flacq; Pte. Vacoas, 3 miles S. of Mahebourg; near Savanne River E. of Souillac (all ANSP). REUNION: (MCZ). MALDIVES ISLANDS: Faro Islet reef, N.W. of Filadu Island, Tiladummati Atoll; between Mafilefuri and Maro Islands, Fadifolu Atoll; Dunidu Island, North Male Atoll; Wala Island, South Nilandu Atoll (all ANSP); Hitadu, Had-dummati Atoll (YPM); Gan, Addu Atoll (YPM; ANSP); Ari Atoll (ANSP). CHAGOS ARCHIPELAGO: Egmont Atoll (Melville, 1909). INDIA: Goa (USNM). CEYLON: Point de Galle (ANSP; RNHL). COCOS-KEELING ISLANDS: Cocos lagoon, North Keeling (both USNM).

Littorina praetermissa May, 1909

(Pl. 325, 343, 344)

Range—Tasmania, Victoria and South Australia.

Remarks—The "neglected" littorine is a distinct and easily recognizable species inhabiting the southeastern Australian region. Considering the narrow range it occupies it is not surprising that it escaped attention until named by May. The

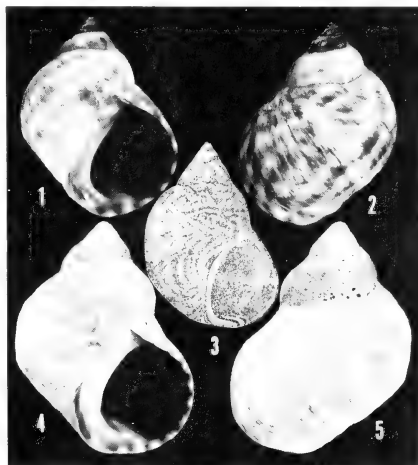


Plate 343. *Littorina (Littoraria) praetermissa* (May)

Figs. 1, 2. Low Head, Tasmania; showing light-brown nuclear whorls and distinctive color pattern (USNM 671215: 11.9 × 7.7 mm.).

Fig. 3. Lectotype, original illustration from Papers and Proceedings Royal Society of Tasmania for 1908, pl. 6, fig. 3; Tasmania.

Figs. 4, 5. Port Fairy, Victoria; large specimen showing considerable wear and/or corrosion (USNM 637353: 16 × 11 mm.).

relationships of *L. praetermissa* appear to lie more closely with the species of the tropical Indo-Pacific than they do with the other Australian species, such as *L. unifasciata*, although the radula of *praetermissa* is similar in the narrowness of the central tooth. It may be distinguished at once from *L. unifasciata* by its coarser spiral sculpture, color markings, less deeply impressed umbilical crescent, and considerably more rounded whorls. The animals also differ in details of verge anatomy.

Habitat—Found in clusters on rock surfaces at and above the high water mark. (Macpherson and Gabriel, 1962).

Description—Shell reaching 16.7 mm. (about .7 inch) in length, globose-turbinate in shape, average obesity about .66 (23 specimens range from .61 to .71); moderately thick in structure, imperforate, developing a rather narrow crescent-shaped area adjacent to columellar callus; sculptured with shallow and relatively widely spaced spiral striae and somewhat irregular axial lines of growth; shell surface rather uneven and bumpy. External ground color of shell grayish white, with usually prominent brown zigzag lines overall. Aperture medium brown with a white band at junction of outer lip and columella; with white markings around inner margin of outer lip. Base hardly flattened, separated from upper part of body whorl by a distinct to obsolete keel at periphery. Whorls 4-5, rounded. Spire considerably less than half the length of shell, convex, produced at an angle of about 72°. Aperture oval in outline; outer lip moderately thick, having its origin high on body whorl above keel so that in some specimens keel enters aperture as a simulated parietal tooth; inner lip nearly straight. Columella yellowish to tannish white, moderately well excavated, with a low tooth-like swelling near junction with outer lip; also usually with a narrow crescent-shaped area on base adjacent to columellar callus. Suture distinct. Sculpture consisting of from 15-17 sometimes indistinct spiral striae on body whorl and from 7-11 on spire whorls; striae fairly distinct in young specimens to indistinct in old individuals; shell surface between striae (i.e. spiral cords) relatively flat; peripheral keel on body whorl moderately formed to obsolete. Shell surface overall rather uneven and bumpy. Axial sculpture consisting of irregular oblique lines of growth. Operculum corneous, rather thin, paucispiral, nucleus well delineated. Periostracum not evident in specimens examined. Nuclear whorls at least partially

decolate in all specimens examined; remaining portions light brown in color, smooth, about 3 in number. Radula littorinid (2-1-1-2) central tooth moderately wide; lateral large and heavy, outer marginal with 11 denticles.

Available rather poorly preserved animals darkly pigmented on surface of tentacles snout and foot. Verge only moderately short and thick; having a simple, truncate basal flap. Nothing is known concerning reproduction and development of this species; probably oviparous, spawning pelagic capsule.

Measurements (mm.)—

length	width	no. whorls	locality
16.7	11.9	4+	South Australia
15.1	9.5	5+	South Australia
14.7	9.5	4+	South Australia
14.1	9.6	4	Port Fairy, Victoria
13.8	8.5	4+	Port Fairy, Victoria
13.1	8.7	5	Low Head, Tasmania
12.0	7.8	5	Low Head, Tasmania
11.7	7.6	4+	Queenscliff, Victoria
9.6	6.3	4+	Port Phillip Heads, Tasmania
9.0	6.3	4	Queenscliff, Victoria

Synonymy—

1909 *Littorina praetermissa* May, Papers and Proceedings of the Royal Society of Tasmania for 1908, p. 57, pl. 6, fig 3 (Tasmania; type deposited in Tasmanian Museum, Hobart: 15 x 11 mm; probable paratypes in Australian Museum, Sydney and in Museum of Comparative Zoology).

Records—SOUTH AUSTRALIA: Robe (NMW); Boat-swain's Point, Nr. Robe (USNM, ANSP, MCZ); Encounter Bay; Adelaide (both ANSP). VICTORIA: Shelly Bay, San Remo (BM(NH)); Phillip Island (MCZ); Sandringham, Port Phillip (ANSP); Port Phillip (AMS); Queenscliff (USNM); Port Fairy (ANSP, USNM, AMS, NMW). TASMANIA: east coast, Tasmania (AMS, paratype); Burnie; Wineglass Bay; Cape Sorell; Opossum Bay; Sandy Cape (all AMS); Low Head (USNM, MCZ); Eaglehawk Neck (AMS, MCZ).

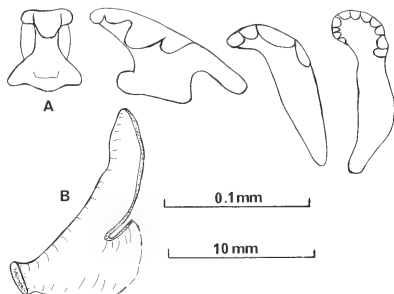


Plate 344. *Littorina (Littoraria) praetermissa* (May)

Fig. A. Radula (upper scale is 0.1 mm.).

Fig. B. Penis (lower scale is 10 mm.); both from Port Fairy, Victoria, Australia, USNM 637353.

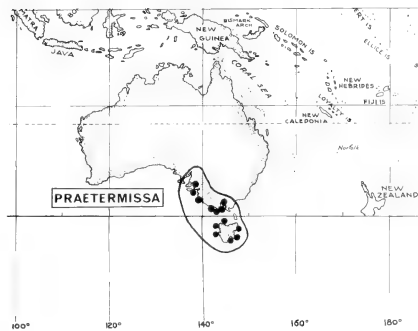


Plate 345. Geographical distribution of *Littorina* (*Littoraria*) *praetermissa* (May) in southern Australia.

Littorina pintado pintado (Wood, 1828)

(Pls. 325, 346, 347)

Range—Southwestern Indian Ocean, from South Africa to Mauritius; in the Western Pacific from Japan through the North Pacific Islands to Hawaii.

Remarks—*Littorina pintado* evidences a very peculiar discontinuous distribution. It occurs in a rather isolated outpost in the southwestern Indian Ocean apparently skips the mainland of southeast Asia and the East Indies and becomes established again in the Western Pacific from whence it is distributed more uniformly eastward to Hawaii. In the eastern part of its range it is recorded only from the North Pacific, but in the Indian Ocean it occurs far south of the equator. This sort of interrupted distribution is difficult to explain unless the concept is accepted of a once more evenly distributed species that for unknown reasons has disappeared from the center of its former range. The possibility of long range rafting or even ship transport cannot definitely be ruled out however. The species is apparently quite hardy and there is a note with two specimens in the USNM collection indicating that they were brought from Hawaii to Los Angeles, California, where they lived for a year without seawater; an almost identical observation was made by Edmondson (1946).

A darker subspecies, *L. pintado schmitti* occurs at Clipperton Island. An apparent analogue of *L. pintado* is *L. pullata* Carpenter of the tropical eastern Pacific. *Littorina tessellata* Philippi of the

tropical western Atlantic, *L. cingulifera* Dunker, and *L. cincta* Quoy and Gaimard of New Zealand initially appear similar to *pintado* but upon closer examination are quite distinct.

Habitat—Lives intertidally on rocky shores and commonly clusters in rock crevices during daylight hours, becoming active at night and crawling about on rocks. Observed to be associated

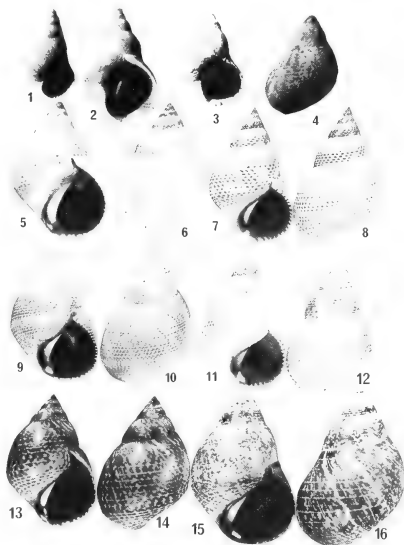


Plate 346. Figs. 1-12. *Littorina* (*Littoraria*) *pintado pintado* (Wood); Figs. 13-16. *L. (Littoraria) pintado schmitti* (Bartsch and Rehder).

Fig. 1. Lectotype of *Turbo pintado* Wood, from Sandwich Isl.; a rather attenuate specimen (BM(NH) 1968368, 17 mm. length.)

Fig. 2. Lectotype of *Littorina serialis* Eyndoux and Souleyet, from Îles Sandwich (MHNP, 18.6 × 11.8 mm.).

Figs. 3,4. Lectotype of *Littorina ambigua* Philippi from Insulae Sandwich (BM(NH) 1968314, 15.9 × 9.7 mm.).

Figs. 5,6. Specimen from Hilo, Hawaii (USNM 339401, 15.5 × 9.7 mm.).

Figs. 7,8. Specimen from Bikini Atoll, Marshall Islands (USNM 585105, 13.4 × 7.6 mm.).

Figs. 9,10. Specimen from Ani Jima, Bonin Islands (USNM 621892, 15.2 × 9.1 mm.).

Figs. 11,12. Specimen from East of Souillac, Mauritius (USNM 637354, 12.2 × 7.3 mm.).

Figs. 13,14. Holotype of *Littorina schmitti* Bartsch and Rehder, from Clipperton Island, eastern Pacific; note dark coloration in this male specimen (USNM 472547, 12.2 × 7.6 mm.; this is specimen figured in original description).

Figs. 15,16. Paratype of *L. schmitti* Bartsch and Rehder, from Clipperton Island, eastern Pacific, female specimen, somewhat corroded, but showing dark coloration (USNM 472546, 14.7 × 8.8 mm.).

with *L. coccinea* and *L. undulata* at Eniwetok and Bikini Atolls, Marshall Islands (personal observations; USNM records) and with *L. picta* in Hawaii (Whipple, 1965; Struhsaker, 1966).

Description—Shell reaching 20.6 mm. (0.8 inch) in length, rather conic-turbinate in shape, average obesity about .60 (18 specimens range from .57-.63); older individuals moderately thick in structure, imperforate, and sculptured with spirally incised lines, overall microscopic wavy spiral threads and oblique axial lines of growth. External color yellowish to purplish gray with an overall pattern of closely spaced reddish-brown streaks or spots; the latter usually arranged in spiral series and only seldom appear axially coordinated; the center of body whorl and anterior half of spire whorls often darker in color. Aperture dark brown, the interstices of outer color pattern showing through as light lines inside outer lip. Base hardly flattened, separated from upper part of body whorl by a rather weak keel at the periphery. Whorls 5-9, moderately rounded. Spire less than half the length of shell, convex, produced at an angle of about 62°. Aperture oval; outer lip thin in young individuals to moderately thick in adults; inner lip weakly concave to nearly straight, its inner margin a white crescent rimmed with dark brown, relatively stout posteriorly but pinched where it joins outer lip at base of columella. Suture moderately impressed; whorls often slightly constricted below suture. Sculpture consisting of about 10-11 spiral striae over surface of spire whorls; from 10-14 striae on body whorl above apertural line and 16-20 below on the base; extra striae often inserted between main striae or

in worn specimens sculpture may be partially obscured. Character of shell surface between striae variable, usually flat but may be raised rounded cords. Entire surface of shell covered with somewhat diffuse microscopic, closely spaced wavy spiral threads not easily detectable in worn specimens. Axial sculpture consisting of rather irregular growth lines which are often associated with dark axial pigmentation streaks. Operculum corneous, paucispiral. Periostracum not evident in specimen examined. Nuclear whorls partially decollate in all specimens examined, remaining portions smooth and glassy; first 2-3 post-nuclear whorls dark brown and sculptured with spiral striae. Radula typically littorinid (2-1-1-1-2).

Animal darkly pigmented on upper surface of tentacles, snout and foot. Verge simple, lacking lateral protuberances, grayish white. Reproduction oviparous; pelagic egg capsule plano-convex in outline, measuring between .16 and .2 mm. in diameter, usually containing a single ovum measuring between .08 and .1 mm. (see Ostergaard, 1950; Whipple, 1965; for details of spawning and development see Struhsaker, 1966).

Measurements (mm.)—			
length	width	no. whorls	locality
20.6	12.3	5+	Midway Id.
19.3	11.0	5+	Midway Id.
19.1	11.0	7+	Chichi Jima, Bonin Ids.
17.0	10.2	5+	Osima Osumi
15.9	10.0	7+	Hawaii
14.7	9.2	5+	Osima Osumi
14.2	8.8	6+	Mauritius
13.0	7.5	7+	Hawaii
12.3	7.4	6+	Mauritius
10.1	6.2	6+	Osima Osumi

Synonymy—

- 1828 *Turbo pintado* Wood, Supplement to the Index Testaceologicus, p. 20, pl. 6, **Turbo** fig. 34 (Sandwich Isl.); lectotype BM(NH) 1968368.
- 1839 *Littorina tenebrata* 'Nuttall' Jay, A Catalogue of the Shells in the Collection of John C. Jay, 3rd ed; p. 73 (Sandwich Isles) [*nomen nudum*]; 1847 [as *Littorina tenebrata* 'Nuttall'] Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, p. 203 [in synonymy of *L. pintado* Wood].
- 1848 *Litorina ambigua* 'Nuttall' Philippi, *Abbildungen und Beschreibungen Conchylien* vol. 3, p. 62, *Litorina*, pl. 7, fig. 6 (Insulae Sandwich); Lectotype in B.M. (NH) 1968314.
- 1852 *Littorina serialis* Eydouard and Souleyet, *Voyage Autour du Monde sur La Corvette La Bonite*, Zoologie, vol. 2, pl. 31, figs 34-36, (Iles Sandwich); lectotype in Museum d'Histoire Naturelle, Paris.
- 1882 *Littorina pindata* Philippi in Weinkauff, *Systematischen Conchylien-Cabinet*, vol. 2, part 9, pp. 63, 70 [error for *L. pintado*].
- 1882 *Littorina ambigua* Reeve in Weinkauff, *ibid.*, p. 70 [error for *L. ambigua*].

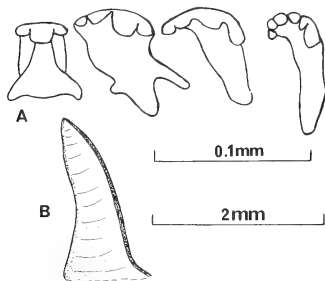


Plate 347. *Littorina (Littoraria) pintado pintado* (Wood)

Fig. A. Radula (upper scale is 0.1 mm.).

Fig. B. Penis; note lack of branches, flaps or glands (lower scale is 2 mm.).

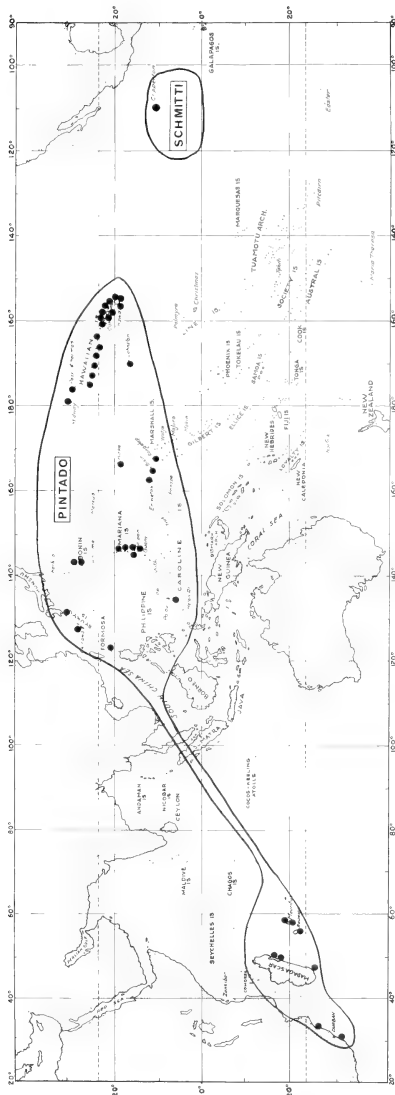


Plate 348. Geographical distribution of *Littorina* (*Littoraria*) *pintado* *pintado* (Wood) in the North Pacific Ocean and in the southwestern Indian Ocean and of the subspecies, *L. pintado* *schmitti* (Bartsch and Rehder), from Clipperton Island, eastern Pacific.

Types—From 17 syntypes of *Turbo pintado* Wood from the Gray collection, the largest is here designated lectotype (see our pl. 346 fig. 1; length 17 mm.; BM(NH) 1968368. The figured specimens of *L. tenebrata* 'Nuttall' Philippi and *L. ambigua* 'Nuttall' Philippi, are here designated lectotypes of these species. The location of the figured specimen of *L. tenebrata* is not known, but that of *L. ambigua* is believed to be in the British Museum (NH) (BM(NH) 1968314; 15.9 x 9.7 mm.; (see our pl. 346 figs. 3, 4). The lectotype of *L. serialis* Eyndoux and Souleyet, here designated, is in the Muséum d'Histoire Naturelle, Paris (see pl. 346 fig. 2; 18.6 x 11.8 mm.).

Records—SOUTH AFRICA: Margate, 11 mi. S. Port Shepstone, Natal. (ANSP). MOZAMBIQUE: Ponta Abril, Delagoa Bay (ANSP). MADAGASCAR: S. of Anivorano, 12 mi. N. of Ambodifototra, W. coast Ile Ste. Marie; S.W. shore of Ile des Nattes, S. of Ile Ste. Marie; Flacourt, Fort Dauphin (all MCZ). MAURITIUS: Pointe Fayette; E.S.E. of Souillac (both ANSP); Souillac S. coast, E. of Souillac (ANSP; USNM). REUNION: (MCZ, NMW). JAPAN: Osumi Islands (USNM). RYUKYU ISLANDS: Shuri; Odonari, both Okinawa (both USNM). PHILIPPINES: Santo Domingo, Batan Island, Batanes Group (USNM). BONIN ISLANDS: (ANSP, MCZ, NMW); Ani Jima; Chichi Jima (both USNM). MARIANAS: Agrigan; W. Pagan (both USNM); Saipan (ANSP, MCZ, USNM); Tinian (MCZ, BPBM; USNM). PALAUS: Angaur (ANSP; MCZ; USNM; SMF). WAKE ISLAND: (USNM; BPBM; ANSP). MARSHALL ISLANDS: Eniwetok; Bikini; Rongelap Atolls (all USNM). HAWAIIAN ISLANDS: Midway (USNM, MCZ, ANSP); Namokulaa, Eastern Islet, Midway Atoll; Pearl and Hermes Reef, Grass Island; Lisianski Island (all BPBM); Laysan (USNM, BPBM); Gardner Island; La Perouse Pinnacle, French Frigate Shoals (both BPBM); Necker Island (BPBM; USNM); Nihoa Island (BPBM); Kaula; Niihau Island (USNM); and many localities on Kauai, Oahu, Molokai, Maui, Lanai, Kahoolawe and Hawaii (see map; ANSP; BPBM; USNM, MCZ). JOHNSTON ISLAND: Sand Island (USNM, MCZ, BPBM).

Littorina pintado schmitti (Bartsch and Rehder, 1939)

(Pl. 346 figs. 13-16)

Range—Known only from Clipperton Island.

Remarks—Hertlein and Emerson (1953) pointed out that a number of marine mollusks which are distributed mainly in the Indo-Pacific have been found on Clipperton Island, a locality which also has strong eastern Pacific faunal affinities. *Littorina schmitti* was described by Bartsch and Rehder as being related to *L. pintado*. The degree of relatedness is considered here to be definitely of subspecific rank, the very distinct differences between *pintado* and *schmitti* apparently having been caused by geographic isolation.

Habitat—Living intertidally on rocks.

Description—Largest available specimen 18.5 mm. (about 0.7 inch) in length, average obesity about .58 (20 specimens range from .54 to .64), somewhat shorter than *L. pintado*, similarly shaped and sculptured, but with darker coloration, the individual color spots tending to be larger and to coalesce, so that many specimens appear to have a dark background with light spots instead of the reverse as in *L. pintado*. Spiral striae usually 7-10 on spire whorls and on body whorl above apertural line, indistinct on the base; shell often marked with white spiral lines, both externally and within aperture; white lines often coincide with striae. Inner lip nearly straight when viewed from aperture; when viewed from aspect of outer lip, columella is thickened and pronouncedly convex at its midpoint.

Measurements (mm.)—

length	width	no. whorls	locality
18.5	10.1	5	Paratype
18.4	9.9	4+	Paratype
17.1	10.5	4+	Paratype
15.7	9.0	5	Paratype
14.9	9.0	6	Paratype
13.9	8.2	5	Paratype
13.0	7.8	5	Paratype
12.6	7.4	7	Paratype
12.2	7.6	6+	Holotype
10.3	6.6	5	Paratype

Synonymy—

1939 *Littorina schmitti* Bartsch and Rehder, Smithsonian Miscellaneous Collections, vol. 98, no. 10 (Publication 3535), p. 9, pl. 2, fig. 4 (Clipperton Island); Holotype: USNM 472547; original measurements of holotype (11.8 x 8.2 mm.) different from those obtained here: 12.2 x 7.6 mm.

Records—*Clipperton Island*: on rocks, south of landing place (Holotype); east side, reef flat (both USNM).

***Littorina sundaica* Altena, 1945**

(Pl. 349, figs. 1, 2)

Range—Java, Indonesia.

Remarks—The “Sunda” littorine is apparently quite distinct species with a rather narrow geographic distribution according to available records, having been reported only from western Java. Due to its small size, however, it may be overlooked easily and when more collections are made in nearby areas of Indonesia, the species may be found more widespread. The dark-brown color, few spirally incised lines of sculpture and single white spiral color band visible internally and externally, together with its

rather narrow shell outline are about the only distinctive characteristics of this species, yet they serve to distinguish it from any other known littorine. The shell of *L. sundaica* bears a slight similarity to the species assigned to *Rissolittorina* Ponder, 1966, *R. alta* Powell, and *mariae* Tension-Woods, especially due to the spiral white band on the base of the shell of all three. However, *Rissolittorina* appears to be a cool water group whereas *L. sundaica* obviously is a tropical species.

Habitat—Not definitely known, but probably on shore rocks.

Description—Shell reaching 8.5 mm. (about $\frac{5}{16}$ inch) in length, elongate-narrow-turbinate in shape, average obesity about .55 (4 specimens range from .53 to .57); shell moderately thick in structure for its size, imperforate, smooth, except for a few spirally incised lines on body whorl and fine growth lines. Overall color of shell nearest to dark reddish brown (ISCC-NBS color number 44) becoming somewhat lighter brown in a diffuse band near suture and aperture edge; with a narrow, white spiral color band on base below periphery also showing in aperture. Base hardly flattened, body whorl subcarinate at periphery. Whorls 5-7, very slightly rounded. Spire more than half length of shell, convex, produced at an angle of about 42°. Aperture subquadrate; outer lip moderately thick, inner lip nearly straight to only slightly concave, glazed with a brown callus, slightly pinched at junction with outer lip. Suture distinct; whorls may be slightly shouldered. Sculpture consists of 2-3 weak incised spiral striae just above periphery and 1-3 below it on base; fine axial and spiral growth lines are visible microscopically. Periostracum not evident. Operculum corneous, paucispiral. Nuclear whorls decollate in all specimens examined. Radula, animal and reproduction unknown.

Measurements (mm.)—

length	width	no. whorls	locality
8.5	4.5	7+	(holotype) Tjilaoet Eureun, Java
7.2	3.8	5+	“Java”
6.0	3.4	5+	Kaledjetan, Bantam, Java
5.5	3.0	6+	“Java”

Synonymy—

1945 *Littorina (Melaraphe) sundaica* Altena, Zoologische Mededeelingen, Leiden, vol. 25, p. 151, fig. 2, (Tjilaoet Eureun, south coast of Java); holotype in Rijksmuseum van Natuurlijke Historie, Leiden, no. 52038.

Records—*JAVA*: (MCZ, USNM); Kaledjetan, Bantam (USNM); Tjilaoet Eureun, (Holotype, RNHL).

Littorina acutispira E. A. Smith, 1892

(Pl. 349, fig. 3; pl. 351, fig. 1)

Range—Known only from coasts of southern Queensland and New South Wales, Australia.

Remarks—This and the preceding species, *L. sundaica* Altena, are placed provisionally in the

subgenus *Littoraria*. More definite placement may be possible upon examination of fresh anatomical material, which has not been available for the present study. The general appearance of *L. acutispira* is littorinoid, but certain features, such as a tendency to form an umbilicus and the yellow bordered aperture which is dark in its interior, resemble some of the Fossaridae, notably *F. atratus* C. B. Adams of the tropical eastern Pacific. Because of the generalized nature of *Littorina*, it is not surprising that some species should resemble more generalized species of other families. The light-colored apertural edge is also seen in *L. africana* and there is a tendency toward this character in *L. unifasciata*.

Habitat—"Common in rock pools" (Smith, 1892).

Description—Shell reaching 7 mm. (about 0.3 inch) in length, elongate-turbinate in shape, average obesity about .57 (7 specimens range from .51 - .63); moderately thick in structure for its size, tending to become umbilicate, sculptured with weak spiral striae and irregular, coarse axial lines of growth. External color variable, from light yellowish brown to dark brown, usually with a wide spiral band of brown to gray encircling body whorl and anterior $\frac{2}{3}$ of spire whorls; speckled on the body whorl with whitish spots.

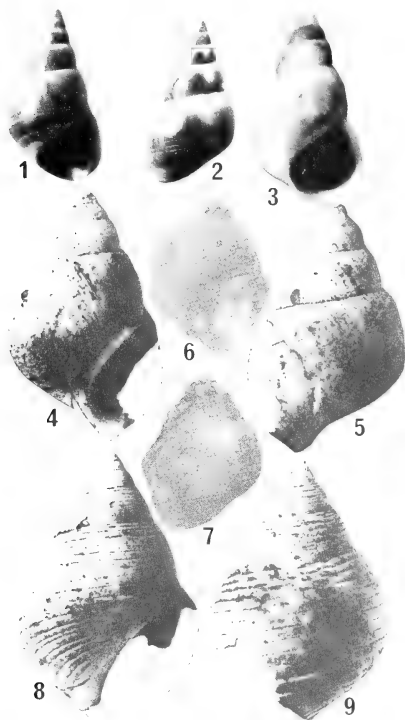


Plate 349. Figs. 1,2. *Littorina (Melarhaphe) sundaica* Altena. Holotype, from Tjilaoet Eureun, S. coast of Java (Leiden Museum no. 52038, 8.4×4.4 mm.).

Fig. 3. *Littorina acutispira* E. A. Smith. Lectotype from Port Jackson, New South Wales, Australia (BM(NH) 91.11.6.216-225, about 7×4 mm.).

Figs. 4,5. *Littorina lucida* Yokoyama. Unique holotype, from Pliocene of Japan (Geological Institute, Imperial University of Tokyo, 5×3 mm.).

Figs. 6,7. *Littorina koiensis* Nomura and Onisi. Unique holotype, from Lower Miocene of Japan (Saitō Hō-on Kai Museum, Sendai, Japan, Reg. no. 21762, 11×8 mm.).

Figs. 8,9. *Littorina adonis* Yokoyama. Unique holotype, from Pliocene of Japan (Geological Institute, Imperial University of Tokyo, 6×4 mm.).

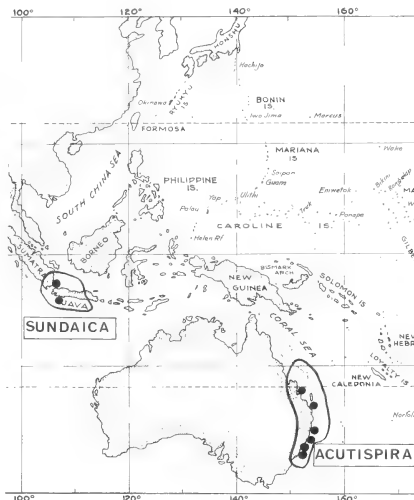


Plate 350. Geographical distribution of the species, *Littorina (Littoraria) sundaica* Altena, in Indonesia, and of *L. acutispira* E. A. Smith, in eastern Australia.

Aperture dark reddish-brown within and on columellar lip; outer lip with a broad white band and a white stripe revolving into it. Base slightly flattened; body whorl weakly carinate. Whorls 4-6, rounded. Spire more than half the length of shell, convex, produced at an angle of from 45-50°. Aperture oval; outer lip moderately thick, inner lip slightly concave, glazed with a brown callus, flattened, and pinched near junction with outer lip; when umbilicus is present there is a trough just outside columellar callus. Suture distinct, whorls hardly shouldered. Spiral sculpture consists of well-spaced, weak spiral striae over surface of whorls; axial sculpture of irregular axial lines of growth. Periostracum not evident. Operculum corneous, paucispiral. Nuclear whorls decollate in all specimens examined. Radula, animal and reproduction unknown.

Measurements (mm)—

length	width	no. whorls	locality
7	3.5	6	lectotype
5.6	3.4	5	All from Port Jackson,
5.6	3.1	5	New South Wales,
5.0	2.6	5	Australia
4.5	2.5	5+	
4.3	2.7	4+	
3.8	2.2	4	

Synonymy—

1892 *Littorina acutispira* E. A. Smith, Proceedings of the Zoological Society of London, part 4, (1891), p. 487, pl. 40, fig. 3 (rock pools, Green Point, Watson Bay, Port Jackson, New South Wales); lectotype BM(NH) 91.11.6.216-225.

Types—One of the 14 syntypes of *L. acutispira* Smith (BM(NH) 91.11.6.216-225) is here chosen as lectotype for the species (see our pl. 349 fig. 3; 7 x 3.5 mm.).

Records—AUSTRALIA: Gladstone; Caloundra, both Queensland (both AMS); Port Macquarie; Catherine Hill Bay; Middle Harbor (all AMS); Port Jackson, all New South Wales (AMS; MCZ; USNM).

***Littorina infans* E. A. Smith, 1892**

(Pl. 351, fig. 2)

Range—New South Wales and Queensland, Australia.

Descriptive Remarks—*Littorina infans* is included provisionally here although its small size and the lack of any real proof of anatomical relationships causes me to consider it more a doubtful species of Littorinidae. Final generic and possibly even family assignment must await further investigation.

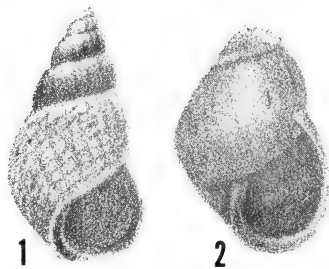


Plate 351. Fig. 1. *Littorina acutispira* E. A. Smith, from Port Jackson, New South Wales, Australia (from original figure in Proc. Zool. Soc., London, for 1891, pl. 40, fig. 3; about 7 x 3.5 mm.).

Fig. 2. *Littorina infans* E. A. Smith, from Port Jackson, New South Wales, Australia (from original figure in Proc. Zool. Soc., London, for 1891, pl. 40, fig. 4; about 3.5 x 2.3 mm.).

Synonymy—

1892 *Littorina infans* E. A. Smith, Proceedings of the Zoological Society of London (1891) p. 488, pl. 40, fig. 4 (Green Point, Watson Bay, Port Jackson [New South Wales, Australia] "found in rocky pools washed by ordinary high tides" (Brazier); syntypes BM(NH); 91.11.6.226-235; original measurements 3.5 x 2.3 mm.

Records—AUSTRALIA: NEW SOUTH WALES: Green Point, Watson's Bay, Port Jackson (Syntypes: BM(NH); AMS); Sussex Haven; Little Coogee Bay; Shark Island. QUEENSLAND: Burleigh Heads; Caloundra; Marouchydore (all AMS).

Littorina kozaiensis Nomura and Onisi, 1940

(Pl. 349, figs. 6, 7)

Range—Lower Miocene of Japan.

Remarks—This species was described as resembling *L. adonis* Yokoyama (see below), but as having a larger number of spiral grooves. The unique holotype (pl. 349, figs. 6, 7, a copy of the original illustration) offers little basis for comparison with Recent species.

Synonymy—

1940 *Littorina kozaiensis* Nomura and Onisi, Japanese Journal of Geology and Geography, vol. 17, nos. 3 and 4, p. 191, pl. 19, fig 6 a,b. (Yosuibori, Simizu, Kozai-mura, Japan); holotype: Saito Ho-on Kai Museum, Register No. 21762; 11 × 8 mm.

Littorina adonis Yokoyama, 1927

(Pl. 349, figs. 8, 9)

Range—Pliocene of Japan.

Remarks—Placed provisionally here in the subgenus *Littoraria*, this species resembles *L. undulata*, although the strong spiral sculpture is also reminiscent of *Littorinopsis*, i.e. *L. scabra*, etc. Unfortunately the outer lip and a portion of the body whorl of the type (pl. 349, figs. 8, 9) are missing and it is difficult to be sure of their exact shape.

Synonymy—

1927 *Littorina adonis* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 8. (Upper Musashino, Koyasu southern Musashi, Japan); (unique holotype in collection of Geological Institute Imperial University of Tokyo: 6 × 4 mm.).

Littorina lucida Yokoyama, 1927

(Pl. 349, figs. 4, 5)

Range—Pliocene of Japan.

Remarks—This species is from the same deposit as *L. adonis* but lacks the deeply incised spiral sculpture. The type of *lucida*, although of approximately the same size as *adonis* is more slender. This type (pl. 349, figs. 4, 5) is also broken, but the columella is complete and the relationship with members of the subgenus *Littoraria* is more easily confirmed than was the case with *L. adonis*.

Synonymy—

1927 *Littorina lucida* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 9 (Upper Musashino, Koyasu southern Musashi, Japan; unique holotype in collection of Geological Institute Imperial University of Tokyo: 5 × 3 mm.).

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus *Littorinopsis* Mörch, 1876

Type: *Littorina angulifera* (Lamarck, 1822)

The subgenus *Littorinopsis* is a small group of mostly tropical species, typified by *L. angulifera*, which are usually ovoviviparous and which show a habitat preference for mangroves or shore vegetation. Individual populations of some species, such as *L. scabra* and its subspecies *L. angulifera*, exhibit a wide range of variation probably due to the geographical isolation imposed by their method of reproduction which tends to restrict gene flow. Nevertheless, within their ranges, these species are widespread possibly because their habitat offers opportunities for rafting of adults.

Shells of species of *Littorinopsis* show strong development of spiral sculpture which in some may form multiple carinae (*L. carinifera*, *L.*

scabra) and there appears to be a tendency for dark coloration and axial color banding and spotting to become strongly developed also. In males the penis is well-developed, with an open but folded sperm duct, a thickened base and a narrower distal filament.

There are three Recent and two Tertiary fossil species of *Littorinopsis* included here. The extremely variable *L. scabra* forms some local populations which have been considered as species. Most of these appear to be only minor genetical or ecotypical variants, not worthy of even subspecific distinction (see *scabra* synonymy). Two species closely related to *L. scabra* (*L. carinifera* and *L. melanostoma*) appear to have developed sufficient genetic constancy to be considered as separate species.

Synonymy

- 1876 *Littorinopsis* Mörch, Malakozoologische Blätter, vol. 23, p. 135 (type-species by original designation *Littorina subangulata* Lamarck [lapsus for *angulifera*]).
 1887 *Lamellilitorina* Tryon, Manual of Conchology, vol. 9, pp. 230, 253 (type-species by subsequent designation, Wenz, 1939: *Littorina* (*Lamellilitorina*) *albicans* Metcalfe [= *L. scabra* Linné]).

Key to Recent Species of Indo-Pacific *Littorinopsis*

1. Columella lip black *melanostoma*
1. Columella lip not black 2
2. Two broad white bands revolving within aperture, shell carinate and with narrow red axial lines or spots *carinifera*
2. Aperture with many fine lines and spotted with brown inside and out *scabra*

***Littorina scabra scabra* (Linne, 1758)**

(Pls. 325, 352, 353)

Range—Pan-Indo-Pacific, from South Africa to southeastern Polynesia.

Remarks—The “rough” *Littorina*, which is one meaning of the Latin name *scabra* (another is “scabby,” which would also fit a brown-spotted shell) is an extremely ubiquitous species throughout the Indo-Pacific wherever there are mangroves or even wood pilings. Its comparatively large size would appear to make it easily visible were it not well camouflaged on mangrove trunks and branches. The relatively long synonymy is a partial indication of its variability. The species produces an almost endless variety of color and sculptural forms from the “typical” dark brown mosaic banded *scabra* to the whitish rather smooth *albicans* described by Metcalfe. The morphological diversity is probably due to the fact that *scabra* is ovoviviparous and produces closely related, inbred populations within which variations or mutations may develop and are perpetuated. The same phenomenon takes place in the Atlantic subspecies, *angulifera* whose biology is similar to *scabra* (Lenderking, 1954; Struhsaker, 1966).

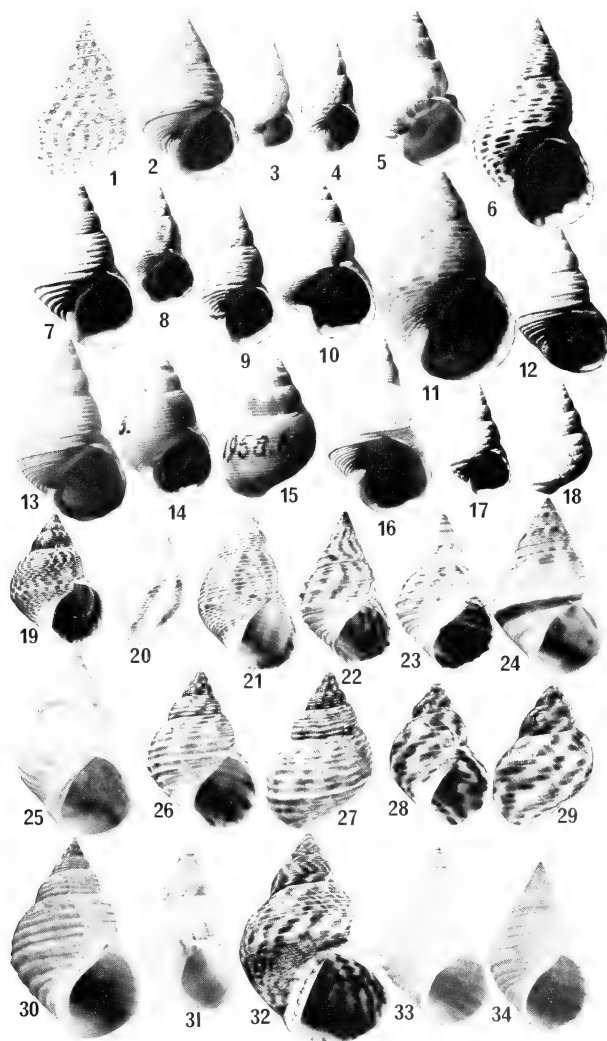
Variations in *L. scabra* generally take the form of yellow and orange color mutants. It may also exhibit normal closely-spaced spiral sculpture to more widely-spaced carinae. These variations occur throughout the geographic range of the species more or less randomly. One variation which appears to be more geographically limited occurs on the north coast of Western Australia and was named *L. sulculosa* Philippi (see pl. 325, fig. 3). Specimens resembling this form were collected from ground rocks in a mangrove swamp on Barrow Island, Western Australia in 1966, and are considered to be ecophenotypes of *L. scabra*, having a habitat different from the latter. Since forms intermediate between *scabra* and *sulculosa* were found at the same locality, *sulculosa* does not appear to have validity as a specific entity.

Differences between *L. scabra scabra* and its Atlantic subspecies *L. scabra angulifera* are difficult to enumerate as they are mostly qualitative: *angulifera* tends to be lighter in color overall, ranging more toward yellow and orange than the darker brown *scabra*; its markings are more diffuse than in most of the latter; the aperture of *angulifera* is narrower, more subquadrate and the columella tends to have a violet hue, while in

Plate 352. *Littorina scabra* (Linné). Showing a range of shell variations.

- Fig. 1. *Helix scabra* Linné (Lectotype figure, from Chemnitz, vol. 11, pl. 210, fig. 2074, about 35 × 21 mm.).
 Fig. 2. *Littorina arboricola* Reeve (Lectotype, from Singapore; BM(NH) 1968321, 31.9 × 25.4 mm.).
 Fig. 3. *Littorina fortunei* Reeve (Lectotype, from China; BM(NH) 1968309, 16.2 × 7.6 mm.).
 Fig. 4. *Littorina flammea* Philippi (Lectotype, from China; BM(NH) 1968310, 16.8 × 7.7 mm.).
 Fig. 5. *Littorina albicans* Metcalfe (Lectotype, from Sarawak, Borneo; BM(NH) 1968355, 18.8 × 10.8 mm.).
 Fig. 6. *Littorina scabra articulata* Philippi (Lectotype, from Mindanao; BM(NH) 1968354, 31.5 × 16 mm.).
 Fig. 7. *Littorina cingulata* Philippi (Lectotype, from “north coast of Australia”; BM(NH) 1968352, 19.4 × 10.7 mm.).
 Fig. 8. *Littorina intermedia* Philippi (Lectotype, from Negros Id., Philippines; BM(NH) 1968353, 14.2 × 7.8 mm.).
 Fig. 9. *Littorina luteola* Quoy and Gaimard (Lectotype, from Port Jackson, Sydney, Australia; MHNP, 16.3 × 9 mm.).
 Fig. 10. *Littorina neucombi* Reeve (Lectotype, from Hawaii; BM(NH) 1968308, 25.3 × 15.1 mm.).
 Fig. 11. *Littorina novaehiberniae* Lesson (Lectotype, from Port Praslin, New Ireland; MHNG, 24 × 13.8 mm.).
 Fig. 12. *Littorina pallescens* Philippi (Lectotype, from Mindanao, Philippines; BM(NH) 1968277, 22.1 × 12.9 mm.).
 Fig. 13. *Littorina philippiana* Reeve (Lectotype, from “Philippines”; BM(NH) 1968307, 29.6 × 16 mm.).
 Figs. 14, 15. *Littorina scabra rhodea* Biggs (Holotype, from Bundar Abbas, Persian Gulf; BM(NH) 1958.6.13.23, ca. 11.5 × 7.5 mm.).

- Fig. 16. *Littorina sieboldii* Philippi (Holotype, from Japan; BM(NH) 1968278, 29 × 15.4 mm.).
 Figs. 17, 18. *Littorina sulculosa* Philippi (Lectotype, from “north coast of Australia”; BM(NH) 1968279, 17.7 × 9.9 mm.).
 Fig. 19. Specimen from Arue, Tahiti (USNM 668338, 15.2 × 9.7 mm.).
 Fig. 20. Specimen from Mweni, Zanzibar (USNM 604470, 15 × 7.3 mm.).
 Fig. 21. Specimen from near Mombasa, Kenya (USNM 215230, 19.9 × 10.5 mm.).
 Figs. 22, 23. Specimen from Proserpine, N. Queensland, Australia (USNM 679498, fig. 22: 23 × 13.2 mm.; fig. 23: 23.4 × 13.2 mm.).
 Figs. 24, 25. Specimens from Po Bui Id., Sandakan, North Borneo (USNM 233252, fig. 24: 20.8 × 11.5 mm.; fig. 25: 22.6 × 11.5 mm.).
 Figs. 26, 27. Specimen from Barrow Id., Western Australia (USNM 691687, 16.1 × 9.7 mm.).
 Figs. 28, 29. Specimen from Sekudu Id., Strait of Johore, Malaysia (USNM 660732, 10 × 6.1 mm.).
 Fig. 30. Specimen from Broome, Western Australia (USNM 637333, 20.2 × 11.6 mm.).
 Fig. 31. Specimen from Santubong, Sarawak, Borneo (USNM 671209, 15.1 × 8 mm.).
 Fig. 32. Specimen from Guam, Marianas (USNM 426452, 39.6 × 22.7 mm.).
 Fig. 33. Specimen from Flat Top Id., near Mackay, Queensland, Australia (USNM 622988, 25.4 × 14.2 mm.).
 Fig. 34. Specimen from Proserpine, Queensland, Australia (USNM 679503, 24 × 12.4 mm.).

Plate 352. *Littorina scabra* (Linné). Explanations on opposite page.

scabra the aperture is more broadly rounded and the columella whitish or stained with brown; in *angulifera* there is often a series of brown spots just within the edge of the outer lip, while in *scabra* the entire interior of the aperture shows the external color, although this is rather variable in both species. Sculptural characters are essentially similar and isolated specimens are difficult to distinguish without comparison. I consider the range of *L. scabra* to be limited to the tropical Indo-Pacific, that of *angulifera* the tropical east and west Atlantic. Some introductions of *L. angulifera* into the east Pacific have taken place in the vicinity of Panama and the notable subspecies *L. scabra abberans* (Philippi, 1846), having a dark brown-rimmed aperture, occurs occasionally in that area.

A possible explanation for the wide range of variation in color of *L. scabra*, in addition to the fact that populations are more reproductively isolated than many other marine snails by reason of being ovoviviparous, is that it is, in effect, largely a tree snail. Extreme color variation is recognized within and between populations of such pulmonate tree snail genera as *Polymita* and *Liguus*. Clench (1968) stated that for tree snails "coloration is apparently non-selective as there must be little ocular predation." When snails leave the ground and ascend trees, they are immediately free of much of the danger from attacks by ground-living invertebrates and mammals which under ordinary conditions may select them for the familiar subdued coloration usually evidenced by many exposed land, freshwater and marine snails. It may be theorized, therefore, that in *L. scabra* color variation is not under the control of selective forces usually exerted upon other species of Littorinidae and is, therefore, freely expressed in many of its populations.

Habitat—Usually found on the trunks and branches of mangroves and on the ground; may be present on dock pilings and on sea walls; not commonly found on shore rocks except in areas from which mangroves are absent.

Description—Shell reaching 43 mm. (about 1¹¹/₁₆ inches) in length [occasionally larger, but often smaller], high-turbinate in shape, average obesity about .57 (15 specimens range from .50-.67); relatively thin in structure, usually imperforate, and sculptured with spiral striae between which on the body whorl are raised, split spiral cords; body whorl subcarinate to carinate at periphery. Color and color pattern variable, typi-

cally a mosaic of brown blotches arranged axially or zigzag or in no apparent pattern; occasional populations with individuals partly or entirely lacking brown pattern and ranging in color from reddish orange through medium brown to yellow and white. Base often moderately flattened, separated from upper part of body whorl by a moderately to well developed keel at periphery. Whorls 6-9, well rounded. Ratios of aperture and spire length to length of shell varying from equal to one exceeding the other. Spire convex, produced at an angle of from 43-57° depending on population. Aperture large, rather broadly rounded in outline; outer lip rather thin even in mature individuals, curving out widely; inner lip usually concave posteriorly (above) slightly convex anteriorly and almost forming a tooth just above where it joins outer lip near base of columella. Apertural portion of columella heavy, usually white or with violet to brown stains. Interior of aperture showing same mosaic color pattern as exterior. Suture distinctly impressed, whorls often showing a weak but differentiated subsutural cord standing out from preceding whorl. Sculpture consists of from 10-12 weak to relatively strong spiral cords with intervening shallow spiral striae; cords may or may not be split by secondary striae. Under magnification close-spaced, fine, wavy spiral threads are present over entire surface. Axial sculpture consists of fine lines of growth; occasionally growth lines are well-developed and some specimens may have spaced axial "ribs;" in some specimens every other spiral cord is suppressed and shell develops strongly carinate appearance. Operculum large, thin, corneous, paucispiral. Periostracum not evident. Nuclear whorls partially decollate in all specimens examined; remaining portions light-brown, spirally sculptured, and appear ornate. Radula littorinoid (2-1-1-1-2). Animal large, darkly pigmented on surfaces of tentacles, snout and foot; ctenidium well-developed in both males and females, serving in latter as partitioned "brood pouch," occupying most of dorsal internal surface of mantle cavity. Penis with greatly thickened base, having lateral thickened appendage with bulbous extremity; penis becoming considerably narrower at tip. Sperm groove open but folded. Reproduction ovoviviparous; eggs released into mantle cavity where held in ctenidial "brood pouch;" usually released in late veliger stage; free-swimming larval life probably very short. Egg size about 0.11 mm.

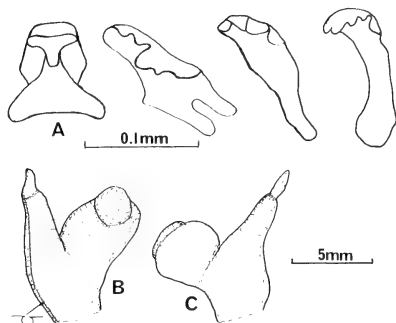
Plate 353. *Littorina scabra* (scabra) (Linné).

Fig. A. Radula of specimen from Sanga Sanga Id, Sulu Archipelago, Philippines, ANSP 230667; upper scale is 0.1 mm.

Figs. B,C. Penis of specimen from Eniwetok, Marshall Ids.; fig. B. view from posterior showing sperm duct (detail indicates deep duct) fig. C. anterior view; specimen relaxed with Propylene Phenoxylol; scale is 5 mm.

Measurements (mm.)—

length	width	no. whorls	locality
43.3	25.3	6	Luzon, Philippines
42.1	23.4	7	Oahu, Hawaii
39.7	22.6	7	Guam
38.2	21.4	8	Barrow Id., W. Australia
35.3	19.9	8	Barrow Id., W. Australia
33.7	18.0	7	Luzon, Philippines
30.7	18.5	7	Buka Id., Gulf of Tomini, Celebes
27.4	16.4	7	Mauritius
24.1	14.4	6	Jordan River, Guimaras Philippines
23.6	11.8	8+	Formosa
20.6	11.6	8	Koh Tau, Thailand
19.8	12.1	7+	Formosa
17.4	10.0	7	Vengurla, India
14.1	7.8	7+	Changanou Strait, Mombasa, Kenya
11.0	6.0	7	Buena Vista, Guimaras Id., Philippines

Synonymy—

- [1705 *Buccinum foliorum* Rumphius, d'Amboinische Rariteit-kamer, p. 98, pl. 29, species Y; prelinnean.]
- 1758 *Helix scabra* Linné, Systema Naturae, ed., 10, vol. 1, p. 770; type locality here designated: Amboina, Moluccas; Lectotype here designated: specimen figured by Chemnitz, vol. 11, pl. 210, fig. 2074.
- 1791 *Buccinum lineatum* Gmelin, Systema Naturae ed. 13, vol. 1, part 6, p. 3493; refers to Knorr, Vergn., 3, pl. 14, fig. 4, here designated lectotype (no locality given).
- 1831 *Littorina novae-hiberniae* Lesson, Voyage Autour du Monde, Coquille, vol. 2, part 1, p. 348 (Port Praslin, Nouvelle-Irlande [Solomon Islands]). Lectotype here designated, specimen ex. Lesson in MHNG: 24 x 13.8 mm).

- 1832 *Littorina luteola* Quoy and Gaimard, Voyage de l'Astrolabe, vol. 2, p. 477, pl. 33, figs 4-7 (Port Jackson, [near] Sydney [Australia]); lectotype here designated one of 7 syntypes in MHNP: 16.3 x 9.0 mm.
- 1846 *Littorina intermedia* Philippi, Proceedings of the Zoological Society of London, part 13 (1845), p. 141 (here restricted to Jimamailan, Negros Id., Philippines); lectotype here selected BM(NH) 1968353: 14.2 x 7.8 mm.; 1847; Abbildungen und Beschreibungen Conchylien, vol. 2, p. 223. *Littorina* pl. 5 fig. 8, (lectotype).
- 1846 *Littorina intermedia punctata* Philippi, *ibid.*, (no locality given in 1846); 1847, *ibid.*; *Littorina* pl. 5, fig. 11 (Tahiti; Elizabeth Island; Natal; Red Sea).
- 1846 *Littorina intermedia articulata* Philippi, *ibid.*, (Swan Point [Western Australia]); 1847, *ibid.*
- 1846 *Littorina intermedia strigata* Philippi, *ibid.*, (Jimamailan, Negros Id. Philippines); 1847, *ibid.*, *Littorina* pl. 5, figs 8-10. (Mergui).
- 1846 *Littorina pallescens* Philippi, *ibid.*, p. 142 (Province of Cagayan de Misamis, Mindanao [Philippines]); lectotype BM (NH) 1968277: 22.1 x 12.9 mm.; 1847, *ibid.*, vol. 3, p. 10 [corrected page] *Littorina* pl. 6, fig. 4.
- 1846 *Littorina sieboldii* Philippi, *ibid.*, (Japonia); holotype in BM(NH) 1968278: 29 x 15.4 mm.; 1847 *ibid.*, p. 9, *Littorina* pl. 6, fig. 3.
- 1846 *Littorina cingulata* Philippi, *ibid.*, (ad oram borealem Novae Hollandiae); lectotype BM(NH) 1968352: 19.4 x 10.7 mm.; 1847, *ibid.*, p. 11, *Littorina* pl. 6, fig. 5.
- 1846 *Littorina sulculosa* Philippi, *ibid.*, (in Ora boreali Novae Hollandiae); lectotype BM (NH) 1968279: 17.7 x 9.9 mm.; 1847, *ibid.*, p. 18, *Littorina*, pl. 6, fig. 10.
- 1847 *Littorina scabra flammulata* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 222, *Littorina* (Panay; Singapore)
- 1847 *Littorina scabra articulata* "Menke" Philippi, *ibid.*, pl. 5, fig. 4, (Mindanao here restricted); lectotype BM(NH) 1968354: 31.5 x 16 mm.)
- 1847 *Littorina scabra punctata* Philippi, *ibid.*, pl. 5, fig. 5. (Masbate; Singapore).
- 1847 *Littorina scabra suturalis* Philippi, *ibid.*, pl. 5, fig. 7 (Kanguruh-Inseln, dem Meersbusen Georgs des Vierten; Canton)
- 1847 *Littorina scabra lutea* Philippi, *ibid.*, pl. 5, fig. 6 (Masbate; Philippines, Canton)
- 1847 *Littorina scabra rubra* Philippi, *ibid.*, refers to Chemnitz [vol. 11, pl. 210] fig. 2075 (Mindoro, Philippines; Canton)
- 1847 *Littorina scabra ventricosa* Philippi, *ibid.*, pl. 5, fig. 8 (China; Mindanao; Tonga Tabu; Neu Irland; Neu Guinea); not *L. ventricosa* Philippi, *ibid.*, vol. 3, p. 15.
- 1847 *Littorina flammea* Philippi, *ibid.*, vol. 3, p. 16, *Littorina*, pl. 6, fig. 21 (China); lectotype BM (NH) 1968310: 16.8 x 7.7 mm.
- 1847 *Littorina sinensis* Philippi, *ibid.*, vol. 3, p. 52, *Littorina* pl. 6, fig. 23 (China).
- 1852 *Littorina albicans* Metcalf, Proceedings of the Zoological Society of London, part 19 (1851) p. 73 (Saravak, Borneo); lectotype BM(NH) 1968355: 18.8 x 10.8 mm.; 1857, Reeve, Conchologia Iconica, vol. 10, pl. 9, figs. 44a, b.
- 1857 *Littorina philippiana* Reeve, *ibid.*, pl. 5, figs 22 a,b (Philippine Islands); lectotype BM(NH) 1968307, 29.6 x 16 mm.
- 1857 *Littorina arboricola* Reeve, *ibid.*, pl. 6, fig 27 a,b (Singapore); lectotype BM(NH) 1968321: 31.9 x 25.4 mm.
- 1857 *Littorina newcombi* Reeve, *ibid.*, pl. 6, fig 28 a,b (Sandwich Islands); lectotype BM (NH) 1968308: 25.3 x 15.1 mm.
- 1857 *Littorina fortunei* Reeve, *ibid.*, pl. 9, figs 42 a,b China); lectotype BM(NH) 1968309; 16.2 x 7.6 mm.

- 1871 *Littorina strigata* Lischke, Malakozoologische Blätter, vol. 18, p. 148 (Nagasaki [Japan]); type: Academy Science, Leningrad?; 1871 Japonische Meeres-Conchylien, vol. 2, p. 73, pl. 5, fig. 22.
- 1871 *Melaraphe (Littorina) blandfordi* Dunker, Malakozoologische Blätter, vol. 18, p. 150 (Rockhampton [Australia]); type in Berlin Museum?
- 1878 *Littorina scabra concolor* Weinkauff, Systematisches Conchylien-Cabinet, vol. 2, part 9, p. 37, pl. 4, figs 8-10 [not fig. 11 as indicated in text = *L. undulata*] (Indo-Pacific) [in part].
- 1878 *Littorina scabra minor* Weinkauff, *ibid.*, pl. 4, figs. 16-18 (Indo-Pacific); refers to *L. intermedia* Philippi and to *L. newkombi* (sic) Reeve.
- 1878 *Littorina newkombi* 'Reeve' in Weinkauff, *ibid.*, pp. 37, 38 [error for *L. newcombi* Reeve].
- 1885 *Littorina scabra tenuis* Nevill, Hand-List of Molluscs in the Indian Museum, part 2, p. 146 (Arakan [Burma]); type in Indian Museum, Calcutta?; not *L. tenuis* Philippi, 1846. [= *L. undulata*].
- 1885 *Littorina pallescens?* *erronea* Nevill, *ibid.*, p. 148 (Singapore); type in Indian Museum, Calcutta?
- 1885 *Littorina filosa subcingulata* Nevill, *ibid.*, p. 149 (Port Jackson [Australia]); type in Indian Museum, Calcutta?
- 1885 *Littorina conica delicatula* Nevill, *ibid.*, p. 149 (Port Canning and False Point [Bengal]); type in Indian Museum, Calcutta?
- 1885 *Leptopoma (?) arduinanium* Heude, Memoires concernant l'Histoire naturelle de l'Empire Chinois, Cahier 3, Notes sur les Mollusques terrestres de la vallee du Fleuve Bleu, p. 95, pl. 25, figs. 8, 8a (ad rupes Tonquineses in portu dictu A-long).
- 1900 *Littorina philippina* von Martens, Biologia Centrali-Americana, Land and Freshwater Mollusca, p. 584; emendation for *L. philippina* Reeve, 1857.
- 1958 *Littorina (Melaraphe) scabra rhodesa* Biggs, Journal of Conchology, vol. 24, no. 8, p. 272 (Bundar Abbas [Persian Gulf]); holotype BM(NH) 1958.6.13.23, ca. 11.5 x 7.5 mm.)

Types—In the original description of *Helix scabra* Linné refers to the Museum Ludovicae Ulricaе, leading one to believe that a specimen under that name was present in that collection. Such a specimen is not contained, however, in the "MLU" of Odhner's unpublished list [1953], nor is *H. scabra* represented in the Linnean Shell Collection in London. Furthermore, in the 12th Edition Linné did not refer to the Ulricaе collection under *scabra*. In order to clarify the concept of *H. scabra*, one of the figures referred to by Hanley (1855), is here designated as lectotype: Chemnitz, Conchylien Cabinet, vol. 11, pl. 210, fig. 2074 (see pl. 352, fig. 1). The specimen represented in that figure may be in the Zoological Museum, Copenhagen. The type locality for *H. scabra* is here designated as Amboina, Moluccas, as no locality was given by Linné.

The location of holotypes and lectotypes of the other synonyms of *scabra* are mentioned in the synonymy where this information is known to me. Types of species described by Philippi in the "Abbildungen" are probably in the Berlin Muse-

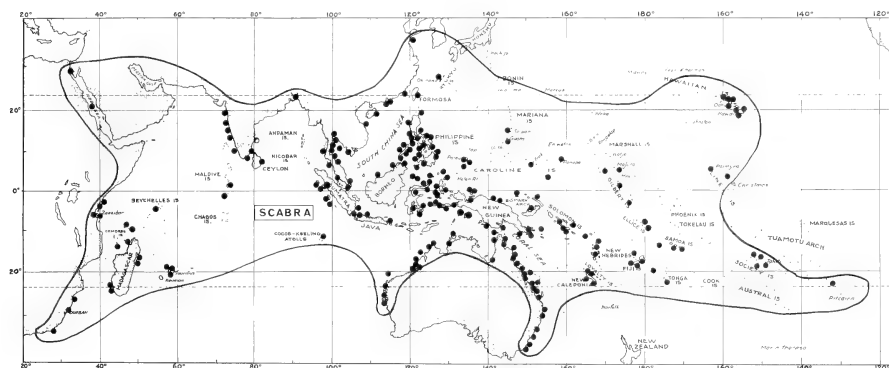
um except in those few cases where I designated as lectotypes the figured specimens found in the British Museum (NH); see Synonymy.

The lectotype of *L. albicans* Metcalfe, mentioned in the synonymy, which is the specimen figured by Reeve, is undoubtedly part of the original syntypic series, as Metcalfe's collection was purchased by Reeve and parts of it were resold (The Athenaeum, No. 1906, May 7, 1864, p. 630).

Records—SOUTH AFRICA: Port Alfred, nr. Grahamstown, Bathurst District, Cape Province (USNM, MCZ); Durban; Isipingo, both Natal (both MCZ). MOZAMBIQUE: Inhaca Island, Delagoa Bay (NMW; ANSP). TANZANIA: Dar es Salaam; 1.5 mi. N.W. of Magogoni; Kendwa Island; Kunduchi; Bagamoyo; Tanga (all MCZ); Mboamagi, 9 mi. S. of Dar es Salaam (USNM); 2 mi. S. by W. of Chwaka, East Zanzibar; Bungi, Kiwani Bay, S.W. Zanzibar; 1 mi. N. of Chukwani, W. Zanzibar (all ANSP); Mbweni, 4 mi. S. of Zanzibar City; Bweju, S.E. Zanzibar (both USNM). KENYA: Mombasa Island (ANSP); Straits at Changanou, 3.75 mi. from Mombasa, Kenya (USNM). MADAGASCAR: S. of Anivorano, 12 mi. N. of Ambodifototra, W. coast of Ile Ste. Marie; Ambodifototra, at causeway to Ilot Mandane, Ile Ste. Marie; S.W. shore Ile des Nattes, S. of Ile Ste. Marie; Soalaly, 16 mi. S. of Tuléar; nr. Grottes de Sarodrano, 10 mi. S.W. of Tuléar (all MCZ); Nossi Be (ANSP; MCZ). SEYCHELLES: Aldabra Island (Y.P.M.; USNM); Menai Island, Cosmoledo Atoll; Anse à la Mouche, Mahe Island; Northwest of Moyenne Island (all YPM). MAURITIUS: Point d'Espy, 1 mi. N. by E. of Poste de Fleury (USNM, ANSP); 1/4 mi. N. of Black River Bay (ANSP). MALDIVES: Male Harbor, Male Atoll; between Maifufuri and Maro Islands, Fadifolu Atoll (both ANSP); Gan, Addu Atoll (YPM; ANSP). INDIA: Bombay (USNM; MCZ); Vengurla, N. of Goa; Goa; Khumta (Kumta), N. of Kanaru; Netravati River, Mangalore; Tuticorin; Adyar River estuary, Madras; Port Canning (all USNM); Cochin Harbor, Kerala; Rameswaram Island, Pamban, Palk Strait (both ANSP); Calcutta (MCZ). CEYLON: (MCZ, ANSP). BURMA: Victoria Point (MCZ). THAILAND: Ko Contee, Ranong (MCZ); Ko Sindar Nua (Chance Island); Ko Phi Phi; Pulau Tanga, Butang Group (all USNM); Songkla (MCZ); Ban Tha Kham; Ko Phluai; Ko Tao (all USNM); Mutapone Island, Chumpon; Ban Hua Hin; Ko Si Chang, 40 mi. S. of Menam River; Bang Poo, Paknam; Ang Hin, Choburi Province; Bang Saen, Choburi Province (all MCZ); Ko Chang; Ko Kut (both USNM). CAMBODIA: Kampot (MCZ). VIETNAM: Saigon (MCZ; MHNP). MALAYSIA: Penang (USNM, MCZ); N.E. corner, Pulau Lumut, Port Swettenham; Pulau Besar, Malacca Strait, S.E. of town of Malacca; Cape Rachau, Straits of Malacca; Sekudu Island, Strait of Johore (all USNM); Singapore (USNM, ANSP, MCZ). CHINA: Kiautschou, nr. Tsingtau, Yellow Sea; Spider Island, Fukien Province; Amoy (all USNM); Hong Kong (BM(NH), USNM, ANSP); Macao; Hainan (both ANSP, JAPAN; Awa (ANSP, MCZ). RYUKYU ISLANDS: (USNM). TAIWAN (USNM, ANSP, MCZ). PHILIPPINE ISLANDS (Many localities; see map). SUMATRA: Moro Id. (SMF); Pulau Melila, S. of Udjung Batu, Banyak Islands; S.E. coast of Pulau Nias; Pulau Bai, Batu Group (all USNM); Padang (MCZ); Pulau Siburu, N. of Sipora; S.W. tip of Sanding Island, Mentawai Islands (both USNM); Tapanuli Bay, Sibolga (ZMA). JAVA: Menscheneter Island (MCZ, ANSP, USNM); Kaledjatan, Bantem (USNM); Djakarta (USNM, ZMA). BALI: Koeta Beach (USNM). BORNEO: Santubong, Sarawak (USNM, MCZ); Kudat Bay (ANSP, USNM); Tajong Aru, Jesselton (USNM); W. Marudu Bay (USNM, ANSP); Po Bui Island, Sandakan; Karamunting, Sandakan; sandy plain, Sandakan Bay; Bohay-dulong Islands (all USNM). CELEBES: Dago Bay, Sangihe Islands; Manado (both MCZ); Likupang, Papajato River; Bukabuka Island, Gulf of Tomini; Limbe Island, Gulf of Tomini (all USNM); Wowoni Id., N. of Butung Island (MCZ);

Labuan Blanda Island, Butung Strait; Labuandata Bay, Gulf of Boni (Bone) (both USNM). MOLUCCAS: Talaud Islands; Morotai Island; Ternate; Kahatola Island, Loloda Islands, N.W. coast of Halmahera; Pajahi Bay, Halmahera Island; Kasirota Bay, Kasirota Island; Batjan Island; Oong Bay, Mandioli Island; Buru Id.; Tengah Island, nr. Buru; Manipa Island (all MCZ); Amboina (ANSP); Koboor, Aru Ids. (SMF); COCOS-KEELING ISLANDS: N.E. end Direction Island (USNM). AUSTRALIA: QUEENSLAND: Darnley Island (MCZ); Murray Island (AMS); Thursday Island, all Torres Strait; mouth of Norman River (both WAM); mud flats nr. Pilot Station, Kurumba; Mapoon all Gulf of Carpentaria; Cape Sidmouth; Burkitt Island, nr. Port Stewart; Three Isles (all AMS); Cooktown (AMS, MCZ); Redlynch (MCZ); Cairns (USNM); Green Island, off Cairns (USNM, MCZ, AMS); Atherton (MCZ); Flying Fish Point (AMS); Dunk Island; Palm Island (both ANSP, AMS); Cape Bowling Green (USNM); Bowen (AMS, MCZ); Hayman Island (AMS); Shute Harbor (USNM); Hamilton Island; Lindeman Island (both AMS); Proserpine (MCZ); Flat Top Island, nr. Mackay (USNM); Percy Island, off Palmerston (MCZ); Yeppoon (AMS); Gladstone (USNM, ANSP); Port Curtis; Port Vernon; Pialba; Urangan (all AMS); Moreton Bay (MCZ); Sandgate, nr. Brisbane (ANSP, AMS); Stradbroke Island (WAM; AMS). NEW SOUTH WALES: nr. Fingal; Broken Bay; Palm Beach and Careel Bay, Pittwater (all AMS); Sydney (MCZ, AMS, USNM, MHP); Botany Bay; Woolawear Bay, nr. Cronulla (both AMS); Wollongong (ANSP); Jervis Bay, Huskisson; Narooma, (both AMS). WESTERN AUSTRALIA: Red Bluff, Shark Bay; Dirk Hartog Island; Herald Bight, N.E. side of Peron Peninsula, Shark Bay; Denham, Peron Peninsula, Shark Bay (all WAM); Carnarvon (WAM, USNM); 20 mi. N. of Cardabia; Monte Bellow Islands (both WAM); Barrow Island (WAM, USNM); Cape Bossut (BPBM); mouth of False Cape Creek, La Grange Bay (USNM, ANSP); Broome (AMS, MCZ, USNM, ANSP); Buccaneer Archipelago; Vansittart Bay (both AMS). NORTHERN TERRITORY: Napier Bay, Melville Id. (WAM); Darwin (MCZ, USNM, ANSP). NEW GUINEA: Hollandia; Selelo Island, off Aitape; Milne Bay; Hilimoi Mission, Milne Bay, Papua (all USNM); Collingwood Bay; Woodlark Island (Murua Island) (both AMS); Port Moresby (USNM, AMS, MCZ, BPBM, ANSP); Oriomo River, Papua; Daru, Papua (both MCZ); Merauke (MCZ, USNM); Fakfak (MCZ); 4 mi. N.W. of Korido Village, Soepiori, Schouten Islands (ANSP); Sorendidori Bay, Soepiori, Schouten Islands (MCZ); Samberbaba, Japen Island; Rainbawi Point, Japen Island; 1/2 mi. E. of Kaiperoi Village, Koeroedoi Island,

Geelvink Bay (all ANSP); Mios Woendi, Schouten Islands (USNM); ADMIRALTY ISLANDS: Koruniat Island (ANSP). BISMARCK: New Britain (AMS); New Ireland (MCZ). SOLOMON ISLANDS: Malaita (MCZ; BPBM); Three Sisters Island; Marava Lagoon, New Georgia (both MCZ); Pavuvu Island, Russell Ids. (USNM); Florida Island (MCZ, USNM); Tulagi, Florida Island (MCZ); Guadalcanal (USNM, AMS). SANTA CRUZ GROUP: Sunday Bay, Vanikoro Island (AMS). NEW HEBRIDES: Oakea, (AMS); Ver, N.E. Santa Maria Id., both Banks Group (USNM); Hog Harbor, Espiritu Santo Island (MCZ); Eromanga (AMS). NEW CALEDONIA: mouth of Ponandou River, E. of Touho (ANSP); Houailoo (BPBM); Ile Nou; Baie du Prony, S. side Mount Dore, nr. Noumea; Ricaudy Reef, Noumea; la Roche Percee, Bourail (all ANSP); Ilot Amedie (AMS). FIJI ISLANDS: Yasawa Islands (USNM); Savasavu, Vanua Levu (MCZ); N. shore Nananu-i-ra Island, (MCZ, USNM); Suva (MCZ; USNM, BPBM); Nadronga (USNM, MCZ); Mbalavu (BPBM); Korolevu (ANSP); Lautoka (MCZ); Nadi Airport, all Viti Levu (USNM); Onega Levu; Ilot Amedie (AMS). FIJI ISLANDS: Yasawa Islands (USNM); Navutu-i-loma (both BPBM). MARIANAS: Saipan (ANSP); Guam (USNM, BPBM). PALAU ISLANDS: Babelthaup Island (USNM, BPBM, ANSP); Koror Island (BPBM); Malakal Pass, W. of Aupapushokaru Island; S.E. end of Eil Malk (both ANSP); Peleliu (BPBM). CAROLINE ISLANDS: Yap Island, (MCZ, ANSP); Moen Island; Dublon Island, both Truk Islands (both BPBM); Ponape (BPBM); Kusaie Island (USNM, BPBM); Kapingamarangi (USNM); MARSHALL ISLANDS: Eniwetok; Arno; Jaluit Atolls (all USNM). GILBERT ISLANDS: Abaiang Island (BPBM, ZMA); Kingsmill Group (ANSP, USNM). HAWAIIAN ISLANDS: Kauai; Oahu; Molokai and Hawaii Islands (Many localities, see map). LINE ISLANDS: Palmyra Island (MCZ, BPBM); Fanning Island, (BPBM). ELLICE ISLANDS: Vaitupu; Nukunaleia (both USNM). WALLIS ISLANDS: btwn, Luania and Fungalei Islands (USNM). TONGA: Velitua Tongatapu (BPBM). SAMOA: Toamua (BPBM); Salafata, both Upolu (ANSP); Pago Pago (BPBM, USNM, ANSP); Fagaitua Bay, both Tutuila (MCZ). SOCIETY ISLANDS: Fannu Bay (USNM); N. end Vaitape; between, Pererau Fai and Araara Pupu, District of Anau, all Bora Bora (both ANSP); Bay Vaioire; around point from Hupu, both Tahaa; Uturoa; Tevaitoa; all Raiatea; Lac Maheva; Port du Bourayne, both Huahine; W. fork of the Opunohu River, Moorea; N.W. of mouth of Nahoata River, Pirae; 9 km. from Taravao, Vairao, Taiarapu Peninsula; Motu Fenuaino, Tautire (all USNM); S. side of Faratea Point, Faa District, all Tahiti (ANSP). GAMBIA ISLANDS: Rikitea, Mangareva; Vaituatai Bay, Mangareva, (both BPBM).

Plate 354. Geographical distribution of *Littorina* (*Littoropsis*)*scabra scabra* (Linne) in the Indo-Pacific faunal region.

***Littorina melanostoma* Gray, 1839**

(Pls. 325, 355)

Range—Southeast coast of India to Borneo.

Remarks—The “Black-mouth” littorine is a very distinctive species within its rather narrow range in south Asia and the East Indies. Its graceful, attenuate outline, dark brown columella

and color pattern offer a combination of characters enabling rapid identification and may qualify this species for the title “most attractive *Littorina*.” Nearest relatives appear to be *L. carinifera* Menke, which also has a fairly restricted distribution in the same general region, and *L. scabra* Linné which is pan-tropical. Among *scabra*, *carinifera* and *melanostoma*, there are

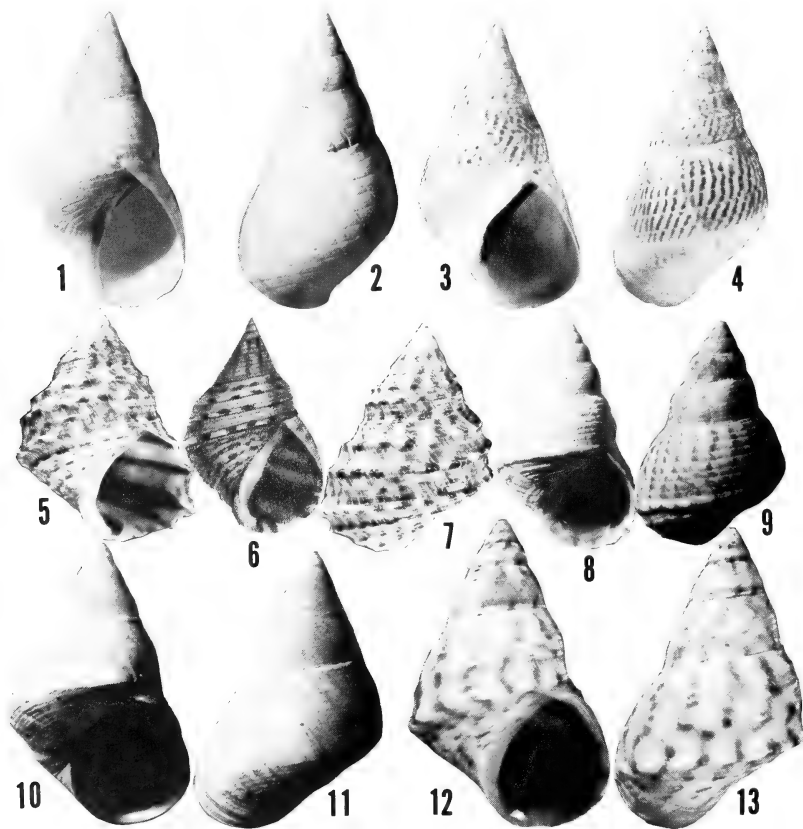


Plate 355. *Littorina melanostoma* Gray (figs. 1-4) *Littorina carinifera* Menke (figs. 5-13).

Figs. 1,2. Lectotype of *L. melanostoma* Gray, from Penang, Malaysia (BM(NH) 1968364, 23.8 × 11.6 mm.).

Figs. 3,4. Port Swettenham, Malaysia (USNM 661028, 28.1 × 13.9 mm.).

Fig. 6. Lectotype figure of *Phasianella carinifera* Menke (from Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, pl. 5, fig. 22; about 21 × 12 mm.).

Figs. 5,7. Sandakan, North Borneo; note similarities to lectotype figure (USNM 658105a, 16.5 × 10.9 mm.).

Figs. 8,9. Lectotype of *Littorina rubropicta* von Martens, from King Id. Bay, Mergui Archipelago, Burma (BM(NH) 57.3.10.140-144, 18.3 × 10.5 mm.).

Figs. 10,11. Lectotype of *Littorina conica* Philippi, from Java (BM(NH) 1968225, 22.4 × 12.7 mm.).

Figs. 12,13. Bombay, India (USNM 90470, 21.6 × 12.4 mm.).

many similarities. All three occupy a similar habitat, anatomical details are remarkably similar, and although spawning behavior has not been verified for *melanostoma* and *carinifera*, they very probably reproduce ovoviviparously.

Habitat—Estuarine areas on mangrove trees and grasses.

Description—Shell reaching 28.2 mm. (about 1 inch) in length, attenuately conical in shape; average obesity about .48 (23 specimens ranged from .44 to .54); relatively thin but strong in structure, imperforate, and sculptured with shallowly incised spiral striae, overall microscopic wavy spiral threads and fine, oblique axial lines of growth. External coloration rather uniform; ground color yellowish white, with closely spaced punctate to elongate-rhomboidal brown markings located between the spiral striae, usually arranged axially but sometimes obliquely or in zigzag pattern; sometimes with white dashes between brown spots; tip of spire often gray; aperture yellowish white or with outer brown color markings partially showing through; columella dark chocolate-brown. Base hardly flattened; only a very weak keel at periphery. Whorls 6-8, usually rather flat-sided. Spire usually somewhat more than half the length of shell, produced at an angle of 42-44°. Aperture oval; outer lip rather thin, often narrowly shouldered; inner lip not greatly thickened, weakly concave, the posterior $\frac{2}{3}$ glazed with dark brown callus, white where it joins outer lip at anterior extremity. Suture weakly impressed. Sculpture consisting of about 6 shallow spiral striae on spire whorls, persisting onto body whorl where as many as 18 may be present over length of whorl; area between striae flattened and each may be divided by single, weak, secondary stria; entire surface covered by fine microscopic wavy spiral threads; floor of striae often appear to be finely, shallowly and closely punctured. Axial sculpture consisting of rather regularly spaced oblique growth lines becoming coarser near outer lip. Operculum large, corneous and paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decoliate in all specimens examined; remaining portions smooth and glassy, light grayish tan in color; succeeding whorls sculptured spirally. Radula typically littorinid (2-1-1-1-2); central tooth broad and low (similar to *L. scabra* and *L. carinifera*).

Animal darkly pigmented on surfaces of tentacles snout and foot. External appearance of animal removed from shell: in female the "cover-

ing-capsule gland complex" (see Fretter and Graham, 1962) located at posterior right of ctenidium, is very distinct, pigmented, and forms a spiral pattern; in male verge is greatly thickened from base to one-half its length; distal portion filamentous; sperm duct deeply folded on floor of mantle cavity and along posterior edge of thickened base of verge and inner edge of filamentous portion. Nothing reported concerning spawning or development of this species, although it is suspected that species is ovoviviparous. In both male and female the ctenidia are greatly enlarged and occupy most of the area of mantle cavity roof, darkly pigmented and conspicuous.

Measurements (mm.)—

length	width	no. whorls	locality
28.2	14.1	8	Port Swettenham, Malaysia
27.8	14.1	8	Chaga, Malaysia
26.1	12.1	8	Nakhorn Si Thammarat, Thailand
25.9	12.9	7+	Nakhorn Si Thammarat, Thailand
24.4	11.5	7	Ko Chang, Thailand
24.0	10.9	7	Port Swettenham, Malaysia
22.6	11.1	7+	Sarawak, Borneo
22.3	12.0	7	Kranji, Singapore
21.9	9.6	8	Burma
21.1	10.1	8	Laem Ngob, Thailand
20.4	10.2	6+	Port Canning, India
20.0	9.7	8	Vietnam
19.2	9.4	6+	Taiwan
14.9	7.2	5+	Hong Kong

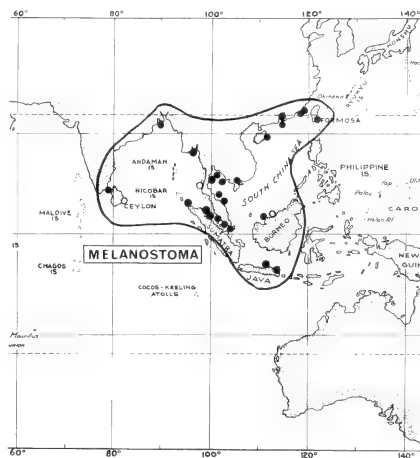


Plate 356. Geographical distribution of *Littorina melanostoma* (Gray) in south Asia and Indonesia.

Synonymy—

- 1839 *Littorina melanostoma* Gray, The Zoology of Captain Beechey's Voyage—in His Majesty's Ship *Blossom*, *Mollusks*, pl. 140 (Indian Ocean; [Penang, Malaysia, here restricted]) lectotype B.M. (NH) 1968364; 23.8 x 11.6 mm.; non *L. melanostoma* A. J. Krynicki, 1837, Bull. Soc. Imp. des Nat. de Moscow, Ann. 1837, No. 2, p. 60, *nomen nudum*.
- 1885 *Littorina melanostoma articulata* Nevill, Hand List of Mollusca in the Indian Museum, part 2, p. 151 (Hong Kong, type in Indian Museum, Calcutta).

Types—*Littorina melanostoma* apparently is one of the species not collected during the voyage of the *Blossom* as Gray gave for a type locality, "Indian Ocean" which the expedition did not reach (Rosewater, 1968). One of the 5 syntypes from Gray's collection is here selected as lectotype: BM(NH) 1968364, 23.8 x 11.6 mm (pl. 355, figs. 1, 2). The type locality is here restricted to Penang, Malaysia.

Records—INDIA: Port Canning (USNM, RNHL); Manali, off Mandapam (MCZ). CEYLON: (E. von Martens, 1887). BURMA: King Island Bay, Mergui Ids. (E. von Martens, 1887). THAILAND: Ko Chang (USNM); Ang Hin (MCZ); Ban Tamru, both Choburi Province (ZMA); Laem Ngob; Pak Phun (both USNM); Pak Paying; Nakhorn Si Thammarat (MCZ). MALAYSIA: N.E. corner of Pulau Lumut, Port Swettenham (USNM); Malacca (MCZ). SINGAPORE: Kranji (ANSP, USNM); CHINA: Hainan, Tsi Mei, Amoy; Hsi-ch'eng, Fukien Province (all ANSP); Castle Peak Bay, Hong Kong (NMW). TAIWAN: (USNM). VIETNAM: Saigon River, Cochinchina (USNM, MCZ). INDONESIA: Palau Weh (RNHL); Telok Niboeng (ZMA); Tandjung Tiram, all Sumatra (ZMA); Djepara (RNHL); Surabaya, both Java (ZMA; RNHL; SMF); Santubong, Sarawak, Borneo (MCZ, USNM).

Littorina carinifera (Menke, 1830)

(Pls. 325, 355)

Range—South and southeast Asia from West Pakistan to the Philippines and Borneo.

Remarks—Of the several forms which have been described as being closely related to *Littorina scabra*, only two appear worthy of recognition as distinct species: *Littorina melanostoma* Gray and *Littorina carinifera* Menke. The latter, "carinate littorine," in its most extreme form, lives up to its descriptive name often having as many as 3-5 rather strong carinae on the body whorl. Variation is considerable, however, and there are populations in which carinae are present only at the periphery. The species may be recognized by its rather pyramidal shape, the color pattern of rather straight to oblique or zigzag reddish axial bands on a yellowish brown background, and by the presence, usually, of dark color bands within the aperture.

Habitat—On bushes or low shrubs along shore; mangrove swamps.

Description—Shell reaching 22.2 mm. (about 0.9 inch) in length, pyramido-conical in shape; average obesity about .63 (23 specimens range from .55 to .71); relatively thick in structure, imperforate, often multiply carinate; otherwise sculptured with well-marked spiral striae, overall microscopic wavy spiral threads (often obscured by wear) and fine, regular, closely spaced axial lines of growth. External coloration rather uniform; ground color yellowish to light-brown, with axial pattern of nearly straight to oblique reddish brown lines. In carinate specimens pattern consists of reddish brown spots primarily on carinae. Aperture grayish white with three or more dark brown bands revolving within; columella white. Base somewhat flattened; periphery, at least, markedly carinate. Whorls 6-7, hardly rounded—to rather flat sided. Spire usually somewhat more than half the length of shell, produced at an angle of 46-72° (depending on specimen). Aperture roundly oval; outer lip rather thin but sometimes thickened within; inner lip not greatly thickened, occasionally with a denticulate swelling near its base, white in color. Suture moderately to well impressed in highly carinate specimens. Sculpture consisting of about 10 often punctate spiral striae on spire whorls, persisting onto body whorl where as many as 20 may be present over length of entire whorl; in non-strongly carinate specimens areas between striae flattened to moderately well rounded as incipient carinae; in strongly carinate specimens at least 3 inter-stria areas raised as rather strong carinae and others may be moderately raised; in these specimens striae are deep furrows and occasionally may be sculptured intrinsically with closely-spaced axial wrinkles; entire surface covered by fine microscopic wavy spiral threads, the latter often obliterated by wear. Axial sculpture consisting of rather regularly-spaced axial growth lines. Operculum moderate in size, corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls partially decollate in all specimens examined; remaining portions smooth, shining, light tan in color; succeeding whorls spirally sculptured.

Animal including radula resembling *L. scabra* and *L. melanostoma*; darkly pigmented on upper surfaces of tentacles, snout and foot. Ctenidial area darkly pigmented showing through mantle; in female "covering-capsule gland complex" (see Fretter and Graham, 1962) located at posterior

right of ctenidium is very distinct, its spiral outline marked with dark pigment; in male verge greatly thickened at base and for about one-half its length; thickened portion terminally bulbous; distal portion filamentous; sperm duct deeply folded, running along posterior edge of verge. Nothing reported concerning spawning or development, but probably ovoviviparous.

Measurements (mm.)—

length	width	no. whorls	locality
22.2	12.2	7	Bombay, India
19.0	11.2	7	Manapla, Negros Occidental, Philippines
18.6	11.2	6	Zamboanga, Mindanao, Philippines
17.8	11.1	7	Iloilo, Panay, Philippines
17.0	10.6	7	Singapore
16.7	11.4	6	Pancol, Palawan, Philippines
16.4	11.2	6	Po Bui Id., Sandakan, North Borneo
14.3	9.0	7	Mangalore, India
13.8	8.4	6+	Silaga R., Samar, Philippines
10.4	7.4	4+	Djakarta, Java

Synonymy—

- 1830 *Phasianella carinifera* Menke, Synopsis methodica Molluscorum, Pyrmont, edition 2, pp. 51, 141 (locality unknown).
 1832 *Littorina perdis* King and Broderip, Zoological Journal, vol. 5 (1831), p. 345 (no locality given).
 1846 *Littorina conica* Philippi, Proceedings of the Zoological Society of London, part 13 (1845), p. 141 (Java); lectotype BM(NH) 1968225; 22.4 × 12.7 mm.; 1847, *Abbildungen und Beschreibungen Conchylien*, vol. 3, p. 9. *Littorina*, pl. 6, figs. 1, 2.
 1855 *Littorina carinifera pyramidalis* Nevill, Hand-List Mollusca in Indian Museum, part 2, p. 151 [*nomen nudum*].
 1855 *Littorina carinifera laevior* Nevill, *ibid.* [*nomen nudum*].
 1887 *Littorina rubropicta* von Martens, Journal of The Linnean Society, Zoology, vol. 21, p. 170, pl. 16, figs. 2 a-f (King Island Bay, Mergui Archipelago); lectotype BM(NH) 87.3.10. 140-144; 18.3 × 10.5 mm.
 1932 *Littorina camifera* Sherborn, Index Animalium, section 2, part 31, p. 638 [error for *L. carinifera*].

Types—According to Dance (1966) Menke's collection was dispersed and therefore, it is most unlikely that the original type specimen of *L. carinifera* can be located. Fortunately Philippi (1847, *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, p. 227, pl. 5, fig 22) apparently had access to Menke's collection and

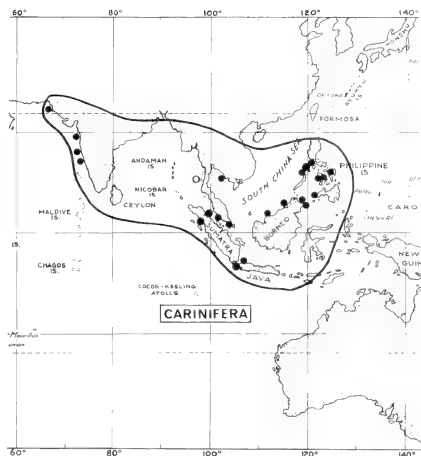


Plate 357. Geographical distribution of *Littorina* (*Littorinopsis*) *carinifera* (Menke) in South Asia, Indonesia and the Philippines.

figured what he called "the original example". That figure is here selected as the lectotype of *Phasianella carinifera* Menke (pl. 355, fig. 6). The type locality is here designated as Negros Occidental, Philippines, one of the localities mentioned by Philippi.

The location of the type-specimen of *L. perdis* King and Broderip is unknown. It may be in the BM(NH) although it was not found during a recent visit. The lectotypes of *L. conica* Philippi and *L. rubropicta* von Martens are in the BM(NH) as mentioned in the synonymy (pl. 355 figs. 8-11).

Records—WEST PAKISTAN: China Creek, Karachi (MCZ). INDIA: Bombay (MCZ, USNM); Vengurla, N. of Goa; Netravati River, Mangalore (both USNM). BURMA: King Island Bay, Mergui Ids. (E von Martens, 1887). THAILAND: Ko Kut (USNM). MALAYA: N.E. corner Pulau Lumut, Port Swettenham; Singapore (both USNM). PHILIPPINES: Medio Island, Galera Bay, Mindoro; Iloilo, Panay; Victoria; Manapla, both Negros Occidental; W. of Catbalogan; Silaga River, both Samar; Zamboanga, Mindanao; Pancol, Palawan (all USNM); Busuanga (RNHL). INDONESIA: Belawan, Sumatra (RNHL, ZMA); Panahatan, Sumatra; Karanganjar, Java (both ZMA); Tandjung Priok, Java (RNHL); Djakarta, Java (ZMA); Santubong, Sarawak, Borneo (both USNM); Labuan, Borneo (NMW, RNHL); Sipitang, North Borneo; Po Bui Island, Sandakan, North Borneo (both USNM).

?*Littorina miodelicatula* (Oyama, 1950)

(Pl. 358, figs. 1-3)

Range—Tertiary of Japan.

Remarks—The species was originally described as resembling some of the Trochidae but Oyama preferred an assignment in Littorinidae near *L. scabra* because of residual color pattern in the fossil and a shape somewhat like that of *L. carinifera*. It is included here somewhat doubtfully as the affinity with Archaeogastropoda seems most likely.

Synonymy—

1950 *Littorinopsis* (*Littorinopsis*) *miodelicatula* Oyama, Geological Survey of Japan, Report no. 132, p. 8, pl. 1, figs 2, 3. (Ueno, Japan; Tertiary Kakebata formation) holotype in collection of Geological Survey of Japan [?]; 8 × 6.7 mm.

***Littorina incisa* Yokoyama, 1927**

(Pl. 358 figs. 4, 5)

Range—Pliocene of Japan.

Remarks—*Littorina incisa* is a relatively small but well-preserved fossil. The excellent illustration given by Yokoyama and reproduced here indicates that this species is probably most closely related to *L. melanostoma* and is quite unlike any other Recent species because of its attenuate shape.

Synonymy—

1927 *Littorina incisa* Yokoyama, Journal of the Faculty of Science, Imperial University of Tokyo, section II, Geology, Mineralogy, Geography, Seismology, vol. 2, part 4, p. 175, pl. 47, fig 8 (Pliocene, Nagaya, Kaga, Japan); holotype in Geological Institute, Imperial University of Tokyo: 5 × 2.5 mm.

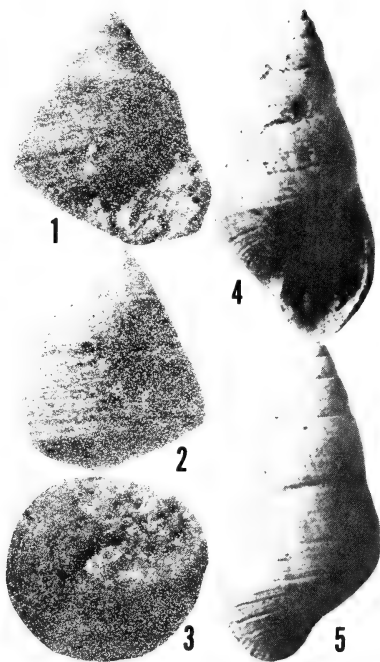


Plate 358. Figs. 1-3. *Littorinopsis miodelicatula* Oyama, from Tertiary, Ueno, Japan (Holotype, from original figures in Report no. 132, Geological Survey of Japan, pl. 1, figs. 3a-c; 8 × 6.7 mm.).

Figs. 4, 5. *Littorina incisa* Yokoyama, from Pliocene, Nagaya, Kaga, Japan (Holotype from original figures; 5 × 2.5 mm.).

Subgenus *Austrolittorina* new subgenus
Rosewater

Type-species: *Littorina unifasciata unifasciata* Gray, 1826

The members of this subgenus are characterized by a predominantly southern ocean and tropical distribution and by the possession of shell and anatomical features generally similar to those of its type-species, *L. unifasciata unifasciata*: a conico-turbinate shell, flattened columella and crescent-shaped area on the adjacent part of the shell; verge with a basal enlargement incorporating a single penial gland containing an accessory flagellum.

***Littorina unifasciata* Gray, 1826**

The *Littorina unifasciata* species complex is represented in the Indo-Pacific faunal region by three entities, the nominate subspecies, *unifasciata* in Australia, and the subspecies *antipoda* in New Zealand and *fernandezensis* in the Juan Fernandez Islands. All closely resemble each other except for size or proportional differences which are the result, probably, of isolation. All members of the subgenus *Austrolittorina* show a preference for the southern ocean south of the equator.

Littorina unifasciata

***subspecies unifasciata* Gray, 1826**

(Pls. 325, 326, 359-361)

Range—Southern coast of Australia, predominantly south of the Tropic of Capricorn, from Carnarvon in the west to Queensland; Lord Howe Island; Tasmania.

Remarks—The nominate subspecies of the *L. unifasciata* group is distinctly a native of the Australian continent occurring extraterritorially only in Tasmania and on Lord Howe Island. The plot of its distribution, if smoothed, would resemble an inverse normal curve (pl. 362); it is restricted almost exclusively to the more southern coasts south of the Tropic of Capricorn. This species has been confused in the literature with *L. mauritiana* Lamarck, although the two are quite distinct morphologically and their geographic ranges are separate (see *mauritiana*).

Both Reeve (1858) and Tryon (1887) considered *unifasciata* to be a synonym of *mauritiana*. Although both may have the single dark band around the whorls upon which the name "*unifasciata*" is based, *mauritiana* is often larger and more elongate, it bears subtle darker patterning and lacks the columellar crescent and penial gland of *unifasciata*.

Habitat—Lives on shore rocks in the spray zone, above high water.

Description—Shell reaching 20.9 mm. (about .8 inch) in length, conical to subturbinat in shape, average obesity about .62 (45 specimens range from .55 - .70); older individuals moderately thick in structure, imperforate, usually developing a flattened, crescent-shaped area adjacent to the columellar callus; sculptured with spiral striae occasionally reinforced with fine brown color lines, spiral, white microscopical textural threads, and irregular, oblique, axial lines of growth. External ground color grayish white to bluish gray, usually the former with a rather diffuse blue-gray band encircling the body whorl and anterior portion of spire whorls; apex light brown. Aperture medium to dark-brown with a prominent white band inside near junction of outer lip and columella. Base somewhat flattened, separated from upper part of body whorl by a low but distinct keel at periphery. Whorls 5-7, rather straight-sided. Spire less than half the length of shell, convex, produced at an angle of about 60°. Aperture oval to subquadrate; outer lip moderately thick, having its origin high on body whorl above keel so that keel enters aperture; outer lip striated internally at edge, reflecting external sculpture; inner lip weakly concave. Columella dark brown to white, shallowly excavated, somewhat rimmed medially, and with a flattened brown to white crescent-shaped area distally on the adjacent base. Suture not deeply impressed. Sculpture consisting of from 6-9 spiral striae on spire whorls, persisting onto surface of body whorl where as many as 12 may be present above the keel; becoming indistinct below keel. Entire surface covered with microscopic, closely spaced rather straight spiral white threads partially imbedded in shell substance and seen through the surface; not detectable in worn specimens. Axial sculpture consisting of rather irregular oblique lines of growth. Operculum corneous, moderately thick, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls decollate in most mature specimens; when present, light brown in color, smooth and about 3 in number;

first post-nuclear whorl similarly colored, but sculptured with spiral striae. Radula littorinid (2-1-1-1-2) central tooth somewhat narrow.

Animal darkly pigmented on surfaces of tentacles, snout and foot. Verge moderately short and thick, yellowish white in color; having a basal

flap with a single penial gland containing an internal hyaline accessory flagellum. Nothing is known concerning the reproduction and development of this species, although probably it is oviparous and spawns pelagic capsules.

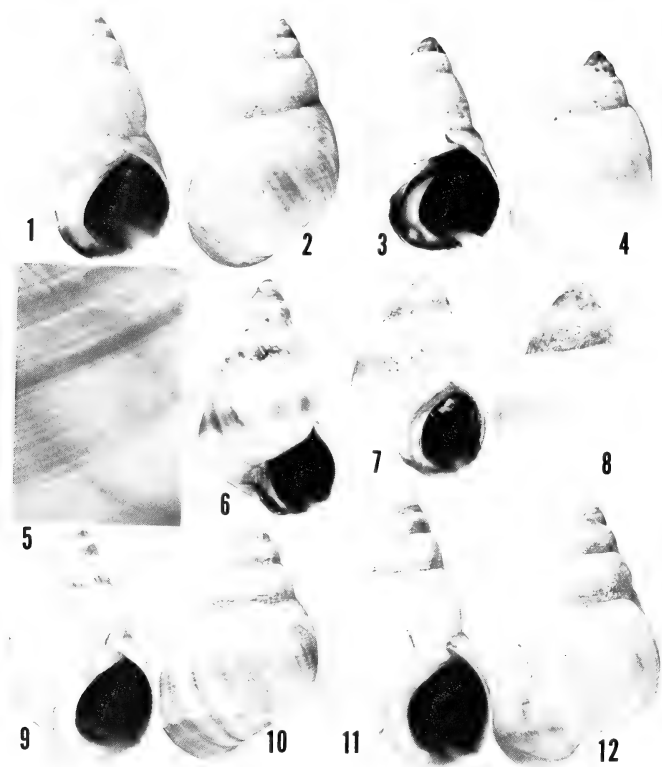


Plate 359. Subspecies of *Littorina* (*Austrolittorina*) *unifasciata* (Gray).

Figs. 1, 2. *L. unifasciata unifasciata* from Port Jackson, New South Wales, Australia (USNM 89472; 20.9 × 12 mm.; note flattened crescent sloped area adjacent to columellar callous).

Figs. 3, 4. *L. unifasciata unifasciata* from Red Bluff, Kalbarri, Western Australia (USNM 691673; 12.7 × 7.6 mm.).

Fig. 5. *L. unifasciata unifasciata* from same locality as Figs. 3, 4; detail of shell surface to show white microscop-

ical textural threads (enlargement of shell area measuring about 1.3 × .8 mm.; young specimen, length 4.9 × 3.2 mm.).

Figs. 6-8. *L. unifasciata antipodum*; fig. 6, from Island Bay, Cook Strait, New Zealand (USNM 671202, 8.7 × 4.8 mm.); figs. 7, 8, from Taipa, Doubtless Bay, North Island, New Zealand (USNM 601974; 7.4 × 4.7 mm.).

Figs. 9-12. *L. unifasciata fernandezensis* from eastern shore Cumberland Bay, Isla Más a Tierra figs. 9, 10, Paratype (USNM 679256, 11.8 × 7.2 mm.); figs. 11, 12, Holotype (USNM 368900, 13.4 × 7.8 mm.).

Measurements (mm.)—

length	width	no. whorls	locality
20.9	11.9	5+	Port Jackson, New South Wales
19.9	12.9	5+	Port Jackson, New South Wales
19.3	11.3	5	Port Jackson, New South Wales
18.2	11.4	6	Kalbarri, Western Australia
17.9	11.6	4+	Kalbarri, Western Australia
16.3	9.5	5+	Robe, S. E. Australia
16.0	9.6	5	Port Denison, Western Australia
15.3	9.3	5+	Port Fairy, Victoria
14.3	9.1	5	Mouth of Murchison River, Western Australia
13.0	7.9	4	near Sydney, New South Wales
12.2	8.1	4	Mouth of Murchison River, Western Australia
10.9	6.5	4+	Queenscliff, Victoria
10.7	7.5	5	Wollongong, N.S.W.
9.4	6.1	4	Coogee Beach, Sydney, N.S.W.
7.3	4.7	5	Coogee Beach, Sydney, N.S.W.
6.4	3.8	3+	Coogee Beach, Sydney, N.S.W.
5.0	3.1	3+	Pearl Beach, N.S.W.
4.9	3.4	3+	between Port Phillip Heads and Cape Otway, Victoria

Synonymy—

- 1826 *Littorina unifasciata* Gray, in P. P. King, Narrative of a survey of the coasts of Australia, vol. 2, Appendix B, p. 483 (Australia [King George Sound, Western Australia, here restricted]); lectotype B.M.(N.H.) 1968373; 16.4 × 10.6 mm.
- 1833 *Littorina diemenensis* Quoy and Gaimard, Voyage de découvertes de l'Astrolabe, vol. 2, part 2, p. 479, pl. 33, figs. 8-11 (rocks of the littoral zone of South Australia, Tasmania and also New Zealand [here restricted to Tasmania]); lectotype in Mus. d'Hist. Nat., Paris; 10.2 × 5.9 mm.
- 1843 *Littorina acuta* Menke, Molluscorum Novae Hollandiae Specimen, p. 9 (Western Australia; type lost); 1844, Zeitschrift für Malakozoologie, Jahr, 1844, p. 57.
- 1847 *Littorina mauritiana crassior* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 165, *Littorina* pl. 3, fig. 17[a] (Australia [here restricted]).
- 1850 *Littorina diemenensis* Gray, Figures of Molluscous Animals, vol. 4, p. 78 [error for *L. diemenensis* Quoy and Gaimard, 1833].
- 1858 *Littorina laevis* 'Philippi' Reeve, Conchologia Iconica, vol. 10, *Littorina*, pl. 17, fig. 95 (locality not given); not *L. laevis* Philippi = *L. mauritiana* Lamarck.
- 1885 *Littorina diemenensis pseudolaevis* Nevill, Hand-List of Mollusca in the Indian Museum, Calcutta, part 2, p. 141, (New South Wales); new name for *L. laevis* Reeve, not *L. laevis* Philippi.

Types—The lectotype of *L. unifasciata* Gray is in the BM(NH), 1968373. The type locality mentioned by Gray, Australia, is here restricted to



Plate 360. Figs. 1,2. Lectotype of *Littorina unifasciata* Gray from Australia [King George Sound, Western Australia] (B. M.(NH) 1968373, 16.4 × 10.6 mm.).

Figs. 3,4. Lectotype of *Littorina diemenensis* Quoy and Gaimard [= *L. unifasciata*] [from Tasmania] (MHNP, 10.2 × 5.9 mm.).

Fig. 5. Lectotype figure of *Littorina antipodum* Philippi, from Abbildungen und Beschreibungen Conchylien, vol. 2, p. 195, pl. 4, fig. 2 (New Zealand, about 7.8 × 4.5 mm.).

King George Sound, Western Australia, one of the localities visited during King's survey. The lectotype of *L. diemenensis* Quoy and Gaimard is in the Paris Museum. It is suspected that the illustration is a composite since there were no specimens in the type lot which fully resembled it. A lectotype was chosen which most closely approximated the illustration, although smaller than the original measurements (10.2 × 5.9 mm. versus approximately 11.3 × 6.8 mm. (5 × 3 lignes)). The holotype of Menke's *L. acuta* may be presumed lost; however the author himself (1844, see *Synonymy*) synonymized his species with *unifasciata* an action which is accepted here as proof of the identity of the species in view of the absence of a type specimen. The type of *L. crassior* Philippi may be in the Berlin Museum; the type of *L. pseudolaevis* Nevill may be in the Indian Museum, Calcutta.

Records—AUSTRALIA: QUEENSLAND: Point Lookout, Stradbroke Island, Moreton Bay (WAM, AMS); Freshwater; Noosa Heads; Caloundra; Coolangatta (all AMS). NEW SOUTH WALES: Byron Bay (MCZ, AMS); Yamba (MCZ); Merewether Beach, Newcastle (WAM); Pearl Beach; The

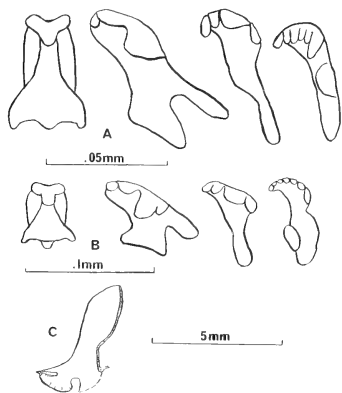


Plate 361. Fig. A. Radula of *Littorina unifasciata unifasciata* from The Entrance, New South Wales, Australia, (USNM 631284; upper scale is .05 mm.)

Fig. B. Radula of *L. unifasciata fernandezensis* from Mas Afuera Id., Juan Fernandez Islands (middle scale is .1 mm.).

Fig. C. Penis of *L. unifasciata unifasciata* from Kalbarri, Western Australia, USNM 691673 (lower scale is 5 mm.).

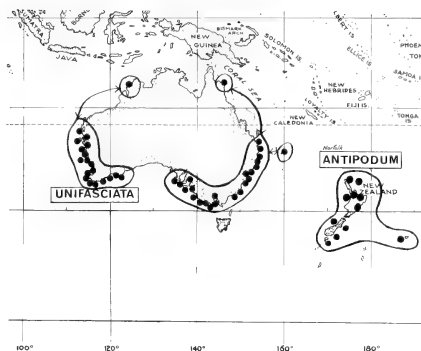


Plate 362. Geographical distribution of *Littorina (Austrolittorina) unifasciata unifasciata* (Gray), in Australia, and of the subspecies, *L. unifasciata antipodum* (Philippi), in New Zealand.

Littorina unifasciata

subspecies antipodum (Philippi, 1847)

(Pl. 359, figs. 6-8, pl. 360)

Range—Islands of New Zealand.

Remarks—The New Zealand species best known as *Littorina oliveri* (Finlay) is without a doubt *L. unifasciata*. Finlay's (1930) comparison of *antipodum* with the typical Australian *unifasciata* best summarizes the differences: "The New Zealand species differs in its smaller shell, higher and more slender spire, with almost straight instead of distinctly convex whorls, notably smaller aperture, and darker more prominent and better defined blue band . . ." It may be theorized that elements of *unifasciata* were carried to New Zealand in the past and that the subspecific differences evolved in response to the new environmental conditions during isolation.

Habitat—On rocks at and above high water mark.

Description—Shell reaching 12.3 mm. (about .5 inch) in length; in general appearance looking much like a diminutive *L. unifasciata unifasciata*, elongate to rather short-conical in shape; average obesity about .59 (21 specimens range from .52-.64). A flattened, crescent-shaped area adjacent to columella callus usually present, but often reduced in size or may be lacking. Sculpture similar to *L. unifasciata unifasciata*. Color band encircling body whorl and anterior portion of

Entrance (both USNM); Putty Beach (AMS); S. shore, Broken Bay, nr. entrance (ANSP); btwn. Newport and Palm Beach (ANSP, USNM; Middle Harbor (AMS); Long Reef, N. of Manly, nr. Sydney (AMS, ANSP); Sydney (MCZ); Port Jackson (USNM, MCZ, AMS, ANSP); La Perouse, Botany Bay (MCZ, ANSP, WAM); Kurnell (AMS); Wollongong (AMS, USNM); Port Kembla (USNM); Merimbula; Two Fold Bay (both MCZ, AMS). VICTORIA: Mallacoota (AMS); Flinders (USNM); Sandringham, Port Philip (ANSP, USNM); Port Philip (ANSP, AMS, MCZ); btwn. Port Philip Heads and Cape Otway (USNM); Barwon Heads (MCZ); Port Fairy (ANSP, USNM, AMS, NMW); Bridgewater Bay (MCZ); Portland (MCZ); TASMANIA: Fischer Island, Bass Strait (AMS); Islets S. of Flinders Island, Bass Strait (WAM); King Island; Bichen; Northwest Long Bay, Port Arthur; Simpson's Bay, D'Entrecasteaux Channel (all AMS); Eagle Hawk Neck; Hobart (both MCZ); Taroona, Derwent River; Grant's Head, Sloop Rocks (both AMS); Low Head (MCZ). SOUTH AUSTRALIA: Boatswain Point (Cape Thomas) nr. Robe (ANSP, USNM, MCZ); Robe (NMW); Encounter Bay (WAM); Port Willunga (both MCZ); Adelaide (USNM); Giles Point, Yorke Peninsula (USNM, MCZ, NMW); Wool Bay (NMW); South Neptune Island, Spencer Gulf (MCZ, AMS). WESTERN AUSTRALIA: Mondrain Island, Recherche Archipelago (WAM); Esperance (AMS); mouth of Pallinup R. Estuary (WAM); Frenchman's Bay, nr. Albany (AMS); Oyster Harbor, nr. Albany, N. of Bayonet Head; Middleton Bay, nr. Albany; Windy Harbor, nr. Northcliffe (all WAM); Cape Leeuwin (AMS); Margaret River (WAM); Wallcliffe, nr. Margaret River (MCZ); Yallingup, Cape Naturaliste; Bunker Bay, Cape Naturaliste (both USNM); Geographe Bay; Bunbury (both AMS); Cottesloe (WAM, AMS); Point Peron, nr. Perth, on boulders; Rottnest Island (both MCZ, AMS); Perth (AMS); Little Anchorage, Leeman; Snag Island, Leeman; Beagle Islands (all WAM); Port Denison (USNM); Greenough River mouth; Harrocks Beach nr. Northampton (both WAM); Red Bluff, Kalbarri, nr. mouth of the Murchison River (WAM, USNM); Eagle Bluff, Freycinet Estuary (WAM); Point Gregory, N.W. Corner Peron Peninsula (WAM); Dirk Hartog Island, (last three all Shark Bay) (AMS); below Quod's Light, N. of Carnarvon (WAM). LORD HOWE ISLAND (ANSP, AMS).

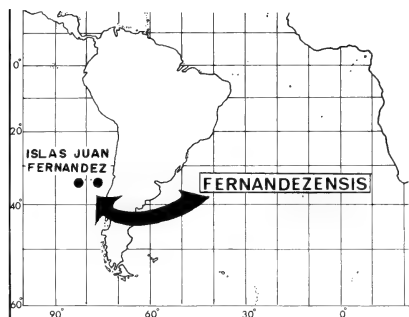


Plate 363. Geographical distribution of *Littorina* (*Austrolittorina*) *unifasciata fernandezensis* Rosewater in the Juan Fernandez Islands, southeastern Pacific.

spire whorls very dark bluish-gray, shell often tinted brown above and below the band. Whorls 4-6, apex usually severely eroded. Radula as in *L. unifasciata*, the central tooth rather narrow.

Animal darkly pigmented on surfaces of tentacles, snout and foot. Verge similar to *L. cincta* and *L. unifasciata unifasciata*: rather short and thick and having a basal mitten-shaped flap which bears a penial gland with an internal hyaline accessory flagellum. Sexually mature males very small. Nothing known concerning reproduction and development, although is probably oviparous and spawns pelagic capsules.

Measurements (mm.)—

length	width	no. whorls	locality
12.3	6.9	6+	Wellington, New Zealand
12.3	6.4	5+	Wellington, New Zealand
10.3	5.6	6+	Port Waikato, New Zealand
10.2	6.0	6	Wellington, New Zealand
9.7	6.0	4+	Christ Church, New Zealand
9.5	6.1	4+	Doubtless Bay, North Island, New Zealand
8.8	5.0	4+	Island Bay, Cook Str. New Zealand
8.5	5.2	5	Napier, New Zealand
7.9	5.0	6	"New Zealand"
5.4	3.2	5	Auckland, New Zealand

Synonymy—

1847 *Littorina antipodum* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, p. 195, *Littorina* pl. 4, fig 2 (New Zealand)

1930 *Melarhaphe oliveri* Finlay, *Transactions of the New Zealand Institute*, vol. 61, p. 224, (Hampden, East Coast of South Island, New Zealand; Holotype in Finlay Collection, Auckland Museum); refers to Suter, 1913, p. 188, and to C. E. R. Bucknill, 1924, "Sea Shells of New Zealand," p. 37, pl. 7, no. 2; not *Melarhaphe zelandiae* Finlay, 1926, which = *L. cincta* Quoy and Gaimard.

Types—The type of *L. antipodum* Philippi may be in the Berlin Museum. The lectotype figure is that of Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, pl. 4, fig 2 (see pl. 360 fig. 5). The holotype of *M. oliveri* Finlay is in the Finlay Collection, Auckland Museum. It should be pointed out here that Finlay (1926) by error described *Melarhaphe zelandiae* intending the name for the New Zealand relative of *L. unifasciata*. However, the type of *zelandiae* proved to be identical with *L. cincta*, another New Zealand species and it was for this reason that Finlay (1930) thought it necessary to describe *M. oliveri* not realizing that Philippi had already described the species over 80 years before.

Records—NEW ZEALAND: NORTH ISLAND: Tauranga (BFBM); Napier; Plimmerton, Wellington; Titahi Beach, in shell sand (all USNM); Island Bay, Cook Strait (AMS, USNM); Worsley Bay, Wellington Harbour (MCZ, USNM); New Plymouth (AMS); Taipa; Doubtless Bay (USNM); Russell, Bay of Islands (MCZ); Hen Island; N.W. point on Motutapu Island (both ANSP); Auckland (AMS, ANSP); W. side Wade River, about 15 mi. N.W. of Auckland (USNM, ANSP); Rangitoto (AMS, ANSP); S. coast, Rangitoto Island (USNM); Manukau Harbor; Port Waikato (both ANSP, USNM); SOUTH ISLAND: Picton; Lyttelton (AMS); Taylor's Mistake, Christchurch (USNM); Porto Bello; Dunedin; Graymouth (all AMS); Stewart Island (ANSP); Chatham Islands (Suter, 1913).

Littorina unifasciata

new subspecies fernandezensis Rosewater

(Pls. 359, 361)

Range—Juan Fernandez Islands, southeastern Pacific.

Remarks—Odhner (1922) reported *Littorina mauritiana* Lamarck from Mas Afuera, Juan Fernandez Islands, and referred to its distribution as extending from Mauritius to New Zealand. In the present study it has been found that *L. mauritiana* is a species restricted to the western Indian Ocean, and that *L. unifasciata unifasciata* and its subspecies *L. u. antipodum*, inhabiting Australia and New Zealand respectively, are quite distinct. The third subspecies of the *L. unifasciata* group, named here, is located geographically quite far from its nearest relative. According to Odhner's

(*ibid.*) analysis the faunal affinities of Juan Fernandez show a closer relationship to South America than to the western Pacific. Further, he found high endemism in the mollusks, indicating long isolation. Nevertheless the *Littorina* from Juan Fernandez is clearly related to *L. unifasciata*, but with sufficient differences to suggest that at least speciation has occurred.

The answer to the question of how *L. unifasciata* and its subspecies became distributed in such widely separated localities will probably never be answered satisfactorily. Although I know of no fossil record, the history of the ancestors of this group probably dates well back into geologic time when land masses and ocean currents are known to have been quite different. It is possible that the group evidences a relict and disjunct distribution from the time when the Antarctic continent was both larger and warmer than it is today. The subspecies living in southern Australia, New Zealand and Juan Fernandez may have evolved from a once more widely distributed species which migrated northward in response to the cooling off of the southern continent. It is also possible that they represent a modern distribution brought about by the predominately western current of the southern ocean. (See discussion of a somewhat similar circumpolar distribution by Abbott, 1968, pp. 183-188).

Littorina unifasciata fernandezensis is very similar to the nominate subspecies, differing in being on the average slightly more slender, although it is not so slender as *L. u. antipodum* (see average obesity in Descriptions of *L. unifasciata* and *antipodum*). There is a superficial similarity in appearance between *L. fernandezensis* and *L. paytensis* Philippi of western South America, but the former lacks the brown color markings, two white bands in the aperture and single strong subsutural stria which are all present in *paytensis*. The two also are members of different subgenera of *Littorina*!

Habitat—Shore rocks.

Description—Shell reaching nearly 18 mm. (about .7 inch) in length, conical to subtruncate in shape average obesity about .60 (52 specimens ranged from .55 - .64); appearance very similar to *L. unifasciata unifasciata*, but more turbinate in shape and less conical; columella not as strongly developed; adjacent crescent-shaped, flattened area persists and may be well developed in some specimens. Spiral striae often strongly impressed, 16-22 striae on body whorl above periphery (14-

16 in *L. unifasciata unifasciata*); striae not reinforced by brown color lines; spiral sculpture sometimes apparent inside edge of outer lip as a series of fine teeth. Color of aperture varying from brown to violet; color band on body whorl often narrower and darker than in *unifasciata*. Animal characters similar to *L. unifasciata unifasciata*

Measurements (mm.)—

length	width	no. whorls	locality
17.6	11.3	3+	Santa Clara Id.
			Islas Juan Fernandez
16.3	10.2	5+	Cumberland Bay, Isla Más a Tierra (paratype)
15.7	9.0	5+	Cumberland Bay
15.3	9.9	4+	Santa Clara Id.
14.4	8.3	6	Cumberland Bay, Isla Más a Tierra (paratype)
13.4	7.8	5	Cumberland Bay, (holotype)
13.4	7.9	5+	Isla Más Afuera
13.2	8.2	4+	Santa Clara Id.
13.0	8.1	5+	Isla Más Afuera
12.8	8.0	4+	Isla Más Afuera
12.4	7.3	6	Isla Más Afuera
11.9	7.4	5	Cumberland Bay, Isla Más a Tierra (paratype)
11.1	6.8	4+	Isla Más Afuera
10.5	6.6	4+	Cumberland Bay, Isla Más a Tierra
10.1	6.5	5+	Isla Más Afuera
9.8	5.7	4+	Isla Más Afuera
8.6	5.4	5+	Isla Más Afuera
7.0	4.3	5+	Cumberland Bay, Isla Más a Tierra (paratype)
6.2	3.7	5+	Cumberland Bay
5.2	3.0	4+	Isla Más Afuera

Types—The holotype was collected by Dr. Waldo L. Schmitt from the littoral zone, east shore of Cumberland Bay, Isla Más a Tierra, Juan Fernandez Islands, in 1926 (USNM 368900); there are 25 paratypes (USNM 679256).

Synonymy—

- 1885 *Littorina penitaria* Wood, in G. Nevill, Hand List of Mollusca in the Indian Museum, Calcutta, part 2, p. 142 (San Juan Fernandez [sic]); [*Nomen nudum*].
- 1922 *Littorina mauritiana* Lamarck, in N. H. Odner, The Natural History of Juan Fernandez and Easter Island, edited by Dr. Carl Skottsberg, vol. 3, part 2, p. 223 (Isla Más Afuera; not *L. mauritiana* (Lamarck, 1822)).

Records—ISLAS JUAN FERNANDEZ: Isla Más Afuera (Odner, 1922); East side of Isla Más Afuera (*Eltanin* Cruise 21, Ann Cohen, Collector; USNM); Holotype and 25 paratypes, east shore Cumberland Bay, Isla Más a Tierra; North Bay, Isla Santa Clara (both collected by W. L. Schmitt in 1926; USNM). Paratypes collected by William Dodd in Del. Mus. Nat. Hist. no. 39221.

Littorina cincta Quoy and Gaimard, 1833

(Pls. 364, 365)

Range—North, South and Stewart Islands, The Snares and Chatham Islands, New Zealand.

Remarks—There is little reason for confusing the two larger species of *Littorina* which inhabit the shores of New Zealand. The closely brown-banded *L. cincta* offers a rather striking contrast

to the lighter, grayish blue *L. unifasciata antipodum* which has a single dark and often diffuse, revolving color band on each whorl. Although there is a superficial resemblance in color pattern between *L. cincta* and *L. pintado*, details of anatomy and of shell morphology confirm their distinctness.

Habitat—On rocks at and above high tide line.

Description—Shell reaching 20 mm. (Suter, 1913; about 0.8 inch) in length, conic-turbinate in shape, average obesity about .60 (23 specimens range from .52-.67); older individuals only moderately thick in structure, imperforate, usually developing an often rather narrow flattened, crescent-shaped area adjacent to columellar callosity; sculptured with often faint spiral striae reinforced by white spiral lines to a varying degree; fine to rather coarse axial lines of growth present. External color pattern consisting of the narrow, white spiral bands with wider medium to dark brown spiral bands interspersed. Aperture usually dark-brown, the narrow white lines showing through inside outer lip, with a broad white band near junction of outer lip and columella. Base hardly flattened, separated from upper part of body whorl by a rather weak keel at periphery. Whorls 5-7, moderately rounded. Spire less than half the length of shell, convex, produced at an angle of about 55°. Aperture oval; outer lip rather thin, inner lip weakly concave. Columella brown to white, shallowly excavated, somewhat rimmed medially and with a flattened crescent-shaped area distally on the adjacent base. Suture impressed. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls smooth and colorless; first 2-3 post-nuclear whorls dark-brown, unsculptured,

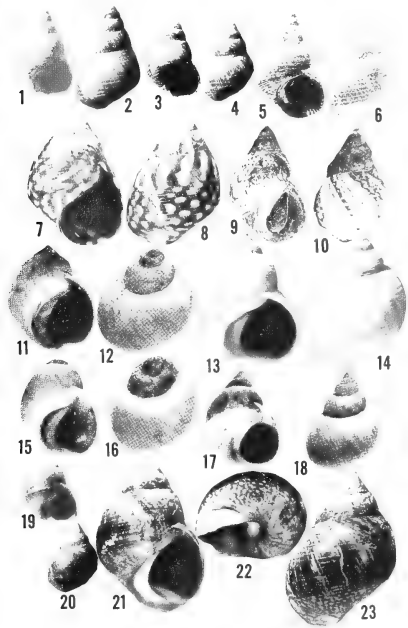


Plate 364. Figs. 1-6, *Littorina (Austrolittorina) cincta* (Quoy and Gaimard).

Figs. 1,2. Lectotype of *Littorina cincta*, from New Zealand (MHNP; 12.1 × 6.8 mm.).

Figs. 3,4. Holotype of *Littorina luctuosa* Reeve (BM(NH) 1968315, 13.7 × 7.6 mm.).

Figs. 5,6. Holotype of *Melarhaphe zelandiae* Finlay (from Transactions of the New Zealand Institute, 1926, vol. 57, pl. 18, figs. 18, 19; 17 × 10.5 mm.).

Figs. 7-10. *Littorina (Austrolittorina) punctata* (Gmelin).

Figs. 7,8. *Littorina punctata*, from 20 km. south of Luanda, Angola, West Africa (USNM 679288; 9.3 × 6 mm.).

Figs. 9,10. Holotype of *Turbo punctatus* Gmelin, Senegal (from Journal de Conchyliologie, 1942, vol. 85, pl. 10, figs. 2a, 2b; MHNP, 17 × 11 mm.).

Figs. 11-16. *Littorina (Austrolittorina) africana* (Philippi).

Figs. 11,12. Lectotype of *Littorina africana*, from Cape of Good Hope, South Africa (Stuttgart Museum (NH): MT 106, 9.8 × 7.3 mm.; photo is from Janus, 1961, Stuttgarter Beiträge zur Naturkunde, no. 70, pl. 3, figs. 1,2).

Figs. 13,14. *Littorina africana*, from Tiger Rocks, Isipingo, Natal, South Africa (USNM 637358, 9.4 × 6.5 mm.).

Figs. 15,16. Lectotype of *Littorina decollata* Philippi, from Natal, South Africa (Stuttgart Museum (NH): MT 107, 5.8 × 4.3 mm.; photo from Janus 1961, Stuttgarter Beiträge zur Naturkunde, no. 70, pl. 3, figs. 3,4).

Figs. 17-23. *Littorina (Austrolittorina) knysnaensis* (Philippi).

Figs. 17,18. Lectotype of *Littorina knysnaensis* from Cape of Good Hope, South Africa, near Knysna River (Stuttgart Museum (NH): MT 108, 9.3 × 6.0 mm.; photo from Stuttgarter Beiträge zur Naturkunde, no. 70, pl. 3, figs. 5,6).

Figs. 19,20. Lectotype of *Littorina picea* Reeve [from South Africa] (BM(NH) 1968320, 6.9 × 4.5 mm.).

Figs. 21-23. *Littorina knysnaensis* from "South Africa"; in fig. 22, basal view, and in fig. 23, note spotted color pattern particularly characteristic of base of shell in this species (USNM 633262, 11.1 × 6.9 mm.).

shining. *Radula* littorinid (2-1-1-1-2); similar to *L. unifasciata* central tooth somewhat narrow.

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verge short and thick, yellowish white in color; having a large basal flap which bears a single penial gland containing an internal hyaline accessory flagellum. Reproduction unknown, probably oviparous with pelagic capsule.

Measurements (mm.)

length	width	no. whorls	locality
19.2	11.0	6+	Wellington Harbour, New Zealand
18.8	10.6	6	Caroline Bay, Timaru, South Island
18.2	9.8	6+	Manukau Harbour
17.1	10.3	4+	Solander Id., Foveaux Strait
16.1	9.3	5+	Auckland
15.4	8.0	6+	Stewart Island
14.4	8.1	5+	Stewart Island
13.5	9.1	4+	Caroline Bay, Timaru, South Island
13.3	8.4	4+	Bay of Islands
11.8	7.1	5	Stewart Island
11.3	7.1	4+	Worser Bay
9.2	6.0	4+	Stewart Island
8.8	5.4	4+	Auckland

Synonymy—

1833 *Littorina cincta* Quoy and Gaimard, Voyage De L'Astrolabe vol. 2, part 2, p. 481, pl. 33, figs 20-21 (New Zealand); lectotype in Museum d'Histoire Naturelle, Paris: 12.1 × 6.8 mm; not *L. cincta* Gould, 1847, Proceedings of the Boston Society of Natural History, vol. 2, p. 252 (from Puget Sound) [= *L. sitchana* Philippi].

1857 *Littorina luctuosa* Reeve, Conchologia Iconica, Vol. 10, *Littorina*, pl. 13, fig. 65 (New Zealand); Holotype BM(NH) 1968315: 13.7 × 7.6 mm.

1926 *Melarhaphe zelandiae* Finlay, Transactions of the New Zealand Institute, vol. 57, p. 375, pl. 18, figs. 18, 19 [description and figs. = *L. cincta*] (Dunedin Harbour; type in Finlay Collection, Auckland Museum, 17 × 10.5 mm.); erroneously proposed as a new species name for *Littorina mauritiana* Lamarck Suter, 1913, p. 188, which = *L. unifasciata antipodum* Philippi (see Finlay, 1930, Transactions of the New Zealand Institute, vol. 61, p. 224).

Types—A lectotype of *Littorina cincta* Quoy and Gaimard is here designated from among three syntypes in the Museum National d'Histoire Naturelle, Paris. (see pl. 364 figs. 1, 2). It is suspected that the figure in L'Astrolabe Atlas is a composite drawing as none of the syntypes match it exactly and it is smaller than the measurement accompanying the description: 12.1 × 6.8 mm. vs 6 × 4 lines [= about 13.5 × 9.0 mm.].

The holotype of *Littorina luctuosa* Reeve is in the British Museum (NH) 1968315 (pl. 364, figs. 3, 4). The type of *Melarhaphe zelandiae* Finlay is in the Auckland Museum (pl. 364, figs. 5, 6).

Records—NEW ZEALAND: NORTH ISLAND: Plimmerton, Wellington (USNM); Worser Bay (USNM, MCZ); Oriental Bay, both Wellington Harbor (USNM); Wanganui (MCZ); New Plymouth (AMS); Doubtless Bay; Russell (both MCZ); Long Beach, both Bay of Islands (USNM); Hen Island, off E. coast Auckland Province (MCZ); Auckland (USNM, ANSP, MCZ); Muriwai Beach (MCZ). SOUTH ISLAND: Lyttelton; Akaroa Banks Peninsula (both AMS); Picton; Kaikoura; Timaru (all MCZ); Caroline Bay, Timaru (USNM); Kartiki, Otago (ANSP); Purakanui, N. Otago (MCZ); Hatchery, Portobello; Pipikariti, Dunedin; Wangaloa; Riverton (all AMS); Wangaloa; Riverton (all AMS); Point Elizabeth (MCZ); Greymouth (AMS, MCZ). FOVEAUX STRAIT: Solander Island (USNM). STEWART ISLAND (USNM, ANSP). CHATHAM ISLANDS. THE SNARES (both Suter, 1913).

Littorina punctata (Gmelin, 1791)

(Pls. 364, 365)

Range—The Mediterranean, West and South Africa.

Remarks—Although not truly a member of Indo-Pacific Littorinidae, *L. punctata* is a tropical species which appears to belong in the subgenus *Austrolittorina* and evidences many characteristics similar to *L. unifasciata*. Its shell is often subtruncate or conical, there is a tendency to

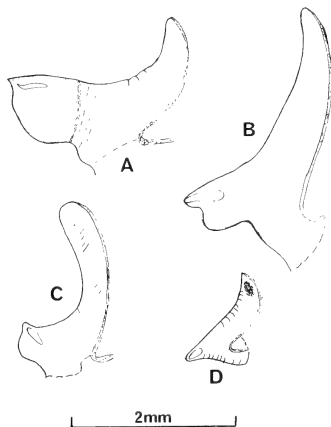


Plate 365. Fig. A. Penis of *Littorina cincta* Quoy and Gaimard, from Plimmerton, Wellington, New Zealand (USNM 671204).

Fig. B. Penis of *Littorina punctata* (Gmelin) from Goreé, Dakar, Senegal (ZMC).

Fig. C. Penis of *Littorina africana* (Philippi) from 11 miles south of Port Shepstone, Natal, South Africa (ANSP 216678); shading indicates pigmentation noted in this and some other specimens.

Fig. D. Penis of *Littorina knysnaensis* (Philippi) from N.E. False Bay, Cape Province, South Africa (ANSP 216643); dark area indicates pigmentation noted in some specimens. All drawn to same scale.

develop a semilunar depression adjacent to the columella, a white band revolving into the aperture, and the verge has a flap with a single hyaline spur. The range of *L. punctata* is quite extensive: from the Mediterranean to South Africa, via West Africa. The species may be recognized readily by the overall pattern of white spots on a dark background from which its name is derived.

It is included here to avoid confusion with Indo-Pacific species whose ranges extend into or are limited to South African waters.

Habitat—Shore rocks, in the spray zone.

Description—Shell may exceed 18 mm. (about 0.7 inch) in length, conical to subtruncate in shape; average obesity about .64 (26 specimens range from .61-.68) moderately thick in structure, imperforate, usually developing a narrow, flattened, crescent-shaped area adjacent to columella callous; sculptured with only moderately well-impressed spiral striae and irregular axial growth lines. External ground color light to dark brown, with an overall pattern of white spots varying in shape from small, compact rhomboidal to elongate. Aperture medium to dark brown with a prominent white band near junction of outer lip and columella. Base somewhat flattened, separated from upper part of body whorl by a low but distinct keel at periphery. Whorls 5-7, rather straight-sided. Spire less than half the length of shell, convex, produced at an angle of about 60°. Aperture oval; outer lip moderately thick, having its origin high on body whorl so that keel enters aperture; inner lip weakly concave. Columella tannish white, shallowly excavated, stout appear-

ing and with a narrow crescent-shaped area on adjacent base. Suture not deeply impressed. Spire sculpture often obscured by wear; 15-17 spiral striae on body whorl above keel, becoming obscure below on base. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls decollate in mature specimens examined. Radula littorinid (2-1-1-1-2) similar to *L. unifasciata*.

Animal darkly pigmented on surfaces of tentacles snout and foot. Verge yellowish white in color moderately short and thick with a basal flap containing a penial gland and hyaline accessory flagellum. Reproductive activity at its greatest during warm months (Tel Aviv, Israel; Palant and Fishelson, 1968). Probably oviparous and spawning pelagic capsules.

Measurements (mm.)—

length	width	no. whorls	locality
18.2	11.1	5+	Ghana
14.0	9.0	5+	Ghana
12.8	7.9	4+	Ghana
11.3	7.4	4+	Valencia, Spain
10.8	6.9	5+	Port Elizabeth, So. Africa
10.5	7.1	4+	Valencia, Spain
9.9	6.4	5+	Alexandria, Egypt
9.0	5.8	4+	Alexandria, Egypt
8.5	5.5	4+	Alexandria, Egypt
7.5	5.1	3+	Alexandria, Egypt

Synonymy—

1791 *Turbo punctatus* Gmelin, Systema Naturae, ed 13, vol. 1, p. 3597 (Senegalia); refers to Adanson, 'Seneg'. Vol. 1, p. 168, t. 12, fig 1, "Le Marnat"; 1942, E. Fischer, et al. Journal de Conchyliologie, vol. 85, p. 268, pl. 10, figs 2a, 2b; Holotype in Museum d'Histoire Naturelle, Paris, 17 × 11 mm.

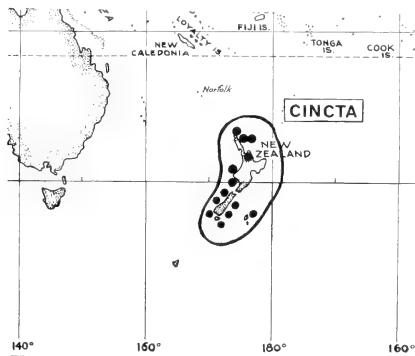


Plate 366. Geographical distribution of *Littorina* (*Austrolittorina*) *cincta* (Quoy and Gaimard), in New Zealand.

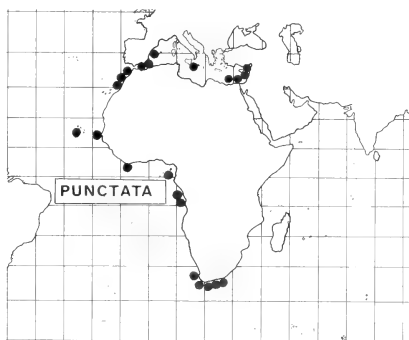


Plate 367. Geographical distribution of *Littorina* (*Austrolittorina*) *punctata* (Gmelin), in the Mediterranean, eastern Atlantic and South Africa.

- 1826 *Tricolia draparnaudii* Audouin, 1826, Explication des Planches, Savigny, Description de l'Egypte, Histoire Naturelle, vol. 1, pt. 4, Mollusques, p. 41, pl. 5, fig. 19 (Egypt); Holotype in Museum d'Histoire Naturelle, Paris.
- 1845 *Littorina pulchella* Dunker, Zeitschrift für Malakozoologie, vol. 2, p. 166 (Loanda [Luanda]); type in Berlin Museum; 1847, Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 198, *Littorina*, pl. 4 fig 8; 1853, Dunker, Index Moll. Guineam, p. 12, pl. 2, figs 11-20.
- 1847 *Littorina syriaca* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 165, *Littorina* pl. 3, figs 21-22 (Ora Syriae [Coast of Syria]); type in Berlin Museum?
- 1858 *Littorina guttata* Reeve, Conchologia Iconica, vol. 10, *Littorina*, pl. 14, fig 76 (St. Vincent, Cape de Verds); not *L. guttata* Philippi [which is *L. meleagris* Potiez and Michaud].
- 1932 *Littorina perplexa* Turton, The Marine Shells of Port Alfred, South Africa p. 133, pl. 28, fig. 960. (Port Alfred, South Africa; type in Oxford University Museum).

Types—*Turbo punctatus* Gmelin is based on Adanson's figure of "Le Marnat". The specimen represented by that figure which is the holotype of *T. punctatus* is in the Paris Museum (pl. 364 fig. 9, 10). The holotype of *T. draparnaudii* Audouin is also in the Paris museum. The types of *L. pulchella* Dunker and *L. syriaca* Philippi may still be extant in the Berlin museum. Reeves *L. guttata* is based on Philippi's figure of a West

Indian specimen. Reeve apparently believed that it was actually the West African species, although the name *L. guttata* Philippi is generally held to be synonymous with the small spotted *L. meleagris*. Young individuals of *L. punctata* appear superficially similar to *L. meleagris* and a comparison of the animal characters of the two is needed. The holotype of Turton's *L. perplexa* is in the Oxford University Museum.

Records—SPAIN: Valencia (SMF; USNM). ITALY: Sicily (USNM). COAST OF SYRIA: (SMF). LEBANON: Beirut (USNM). ISRAEL: Tel Aviv (Palant and Fishelson, 1968). EGYPT: Alexandria (USNM). ALGERIA: Oran (USNM). MOROCCO: Mellilla; Tangier; Casablanca (all USNM); Essaouira (SMF). SENEGAL: Goree (SMF; ZMC). CAPE VERDE IDS: Mindelo, Sao Vicente (USNM). LIBERIA: Cape Palmas. FERNANDO POO: Santa Isabel. CONGO REPUBLIC: Banana R. mouth (SMF). ANGOLA: Ambrizete (SMF); 20 km. S. of Luanda (USNM). SOUTH AFRICA: Langebaan, Saldanha Bay; Dassen Id.; Table Bay; False Bay; Hermanus; Breede R. mouth; St. Sebastian Bay; Still Bay; Mossell Bay; Knysna (all K. H. Barnard, 1963); Port Elizabeth, Algoa Bay (MCZ; USNM).

Littorina africana (Philippi, 1847)

(Pls. 364, 365)

Range—South Africa, from the west side of Cape Peninsula, to southern Mozambique; Madagascar.

Remarks—*Littorina africana* is distinct from, but apparently closely related to, *L. knysnaensis*. Both species occur on the south coast of Africa. The appearance of its shell and its anatomy also show similarities to other southern ocean species, *L. unifasciata*, *L. unifasciata antipodum* and *fernandezensis* and *L. cincta* of Australia and New Zealand. The shell of *L. africana* differs from these species in its development of comparatively strong spiral sculpture (although some individuals appear almost smooth); anatomically its verge is pigmented and the basal flap relatively more pointed. Although Janus (1961) stated that the South African species *L. decollata* Philippi is distinct from *L. africana* the examination of large series and a study of their ecology would be necessary to settle questions regarding differences. Material examined during the present study indicates that the two are identical. Tryon (1887) considered this to be the case and acting as first reviser chose *L. africana* as the senior synonym in spite of the obvious page priority of the name *decollata*.

Habitat—On rocks in the splash zone.

Description—Shell reaching 13.5 mm. (about .5 inch) in length, short-turbinata to subglobose in shape, average obesity about .69 (10 specimens range from .63-.77); older individuals only

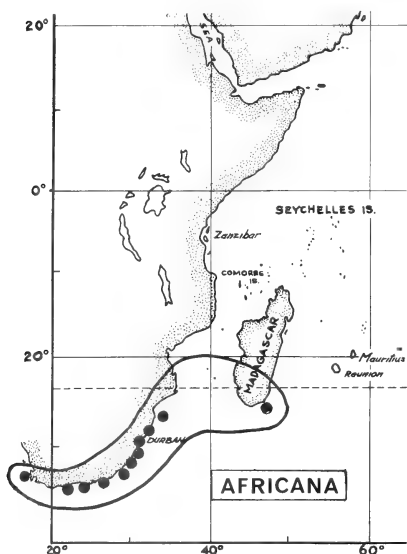


Plate 368. Geographical distribution of *Littorina* (*Austrolittorina*) *africana* (Philippi), in South Africa and Madagascar.

moderately thick in structure, imperforate, usually developing a narrow, flattened crescent-shaped area adjacent to columellar callous; sculptured with closely-spaced, raised spiral threads of varying widths and irregular, sometimes coarse axial lines of growth (sometimes without strong spiral sculpture). External ground color grayish-white, with a diffuse bluish gray band encircling the body whorl and on anterior portions of spire whorls. Aperture medium to dark brown with a prominent white band near junction of outer lip and columella and another often obscure band high in aperture at junction of outer lip and body whorl. Base somewhat flattened, separated from upper part of body whorl by a low rather indistinct keel at periphery. Whorls 3-5, rounded; spire usually much eroded, considerably less than half the length of shell, convex, produced at an angle of about 66°. Aperture widely oval; outer lip moderately thick, having its origin quite high on body whorl, above keel, so that keel enters aperture. Columella usually brown with a lighter somewhat rimmed medial edge, moderately wide and excavated anteriorly, and with a flattened to excavated, brownish, crescent shaped area distally on the adjacent base. Suture impressed. Sculpture consisting of closely-spaced, raised spiral threads of varying widths; wider threads usually separated by 2-4 narrow threads, disappearing on base and on eroded spire, and sometimes appearing entirely smooth. Axial sculpture consisting of occasionally coarse, irregular growth lines. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Radula littorinid (2-1-1-1-2) central tooth somewhat narrow similar to *L. unifasciata*.

Animal darkly pigmented on surfaces of tentacles, snout, foot and on edge of mantle. Verge also darkly pigmented distally, fairly long and club-shaped; having a basal flap which bears a single penial gland containing a hyaline accessory flagellum. Nothing is known concerning the reproduction and development of this species although probably it is oviparous and spawns pelagic capsule.

Measurements (mm.)—

length	width	no. whorls	locality
13.5	8.4	4	Fort Dauphin, Madagascar
10.7	7.4	3+	South Africa
10.5	7.0	3+	Margate, Natal
9.9	6.7	4	Natal
9.9	7.3	5	Natal
9.7	6.7	4	Natal
9.6	6.4	4	Isipingo, Natal
9.0	5.7	4	Umhlali River, Natal
8.6	6.6	4	South Africa
8.2	5.9	3+	Inhaca Island, Mozambique
7.2	5.0	3+	Margate, Natal

Synonymy—

- 1847 *Littorina africana* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, part 7, p. 199, *Littorina*, pl. 4, fig. 10 (Caput Bonae Spei [Cape of Good Hope, South Africa]; lectotype in Stuttgart Museum (N.H.), catalogue number MT 106; 9.8 × 7.3 mm. (Janus, 1961); 1848, Krause, *Die Sudafrikanischen Mollusken*, p. 102; 1858, Reeve, *Conchologia Iconica*, vol. 10, *Littorina*, pl. 8, figs 37 a, b.
- 1847 *Littorina decollata* Philippi, *ibid.*, p. 196, pl. 4, fig. 3 (Ora Natal Africae [Coast of Natal, South Africa]; lectotype in Stuttgart Museum (N.H.), catalogue number MT 107; 5.8 × 4.3 mm. (Janus, 1961); 1848, Krause, *ibid.*, p. 102.

Types—Lectotypes of *L. africana* and *L. decollata* are in the Staatlichen Museum für Naturkunde, Stuttgart, Germany, and were designated from Krauss material by Janus (1961). Philippi listed "Cape of Good Hope" as type locality for *L. africana* and "coast of Natal" for *decollata*. Krauss specified "Algoa Bay" for *africana* which may be construed as a restriction of Philippi's type locality. Janus listed "Algoa Bay" and "Natal" as the type localities of the lectotypes of *africana* and *decollata* respectively.

Records—SOUTH AFRICA: W. Cape peninsula opposite Simonstown; Robberg, Plettenberg Bay (both ANSP); Cape Recife; Port Alfred (both MCZ); East London, mouth of Nahoon River; Second Beach, Port St. Johns, Pondoland; Port Edward, Natal; Margate, 11 mi. S. Port Shepstone, Natal (all ANSP); Tiger Rocks, Isipingo, Natal (USNM; NMW); Durban, Natal (MCZ; USNM); mouth of Umhlali River, Natal. MOZAMBIQUE: Inhaca Is. Delagoa Bay (both USNM). MADAGASCAR: Pointe Ibanona, Fort Dauphin (MCZ).

***Littorina knysnaensis* (Philippi, 1847)**

(Pls. 364, 365)

Range—South Africa, from Lambert's Bay, west coast to Natal.

Remarks—The "*Knysna*" littorina is quite distinctive and relatively easily distinguished from other South African species. "Typical" specimens exhibit a fairly prominent keel, flattened sculpture and brownish and tan coloration with whitish spots. The spots are most clearly observable above and below the wide brown peripheral color band. There is similarity, however, between the verges of *L. knysnaensis* and *L. africana*. Where differences in male anatomy are very slight, habitat differences or physiological barriers may operate in preventing cross fertilization between the species (see Palant and Fishelson, 1968). This species occurs in part outside the range of other South African *Littorina*, being the dominant and/or only South African species on the west coast and becoming rare farther north on the east coast (Stephenson et al, 1940; Stephenson, 1947). It is of course similar in part to *L. punctata* in its spotted coloration, but differs in color pattern distribution and in shell form.

The form *L. africana tryphena* Bartsch was based on beach worn and anomalously high-spired specimens whose appearance is very different. Nevertheless, *tryphena* is an absolute synonym of *knysnaensis*.

Habitat—Intertidal on rocks and in crevices of seawalls.

Description—Shell reaching 13.6 mm. (about 0.5 inch) in length, turbate in shape, average obesity about .64 (21 specimens range from .56-.70); older individuals only moderately thick in structure, imperforate, usually developing a narrow flattened, crescent-shaped area adjacent to columellar callous; sculptured with spiral striae, between which surface of shell is flattened, and closely-spaced rather regular oblique axial lines of growth; at times spiral and axial sculpture tend to produce a reticulated pattern. External color mahogany brown in a wide band above peripheral keel, lighter near suture and on the base, with whitish spots and streaks especially on base. Aperture dark-brown with a white band near junction of outer lip and columella. Base distinctly flattened, separated from upper part of body whorl by a raised keel at periphery. Whorls 3-5, somewhat flattened; spire usually eroded, less

than half the length of shell, convex, produced at an angle of about 66°. Aperture oval; outer lip moderately thick, having its origin quite high on body whorl, above keel, so that keel enters aperture. Columella brown, but sometimes cream-colored, with a rather weakly rimmed medial edge; moderately wide and excavated anteriorly, and with a flattened to excavated, brownish to cream colored crescent shaped area distally on the adjacent base. Suture moderately impressed. Sculpture consisting of about 9 spiral striae on penultimate whorl of spire (surface of younger whorls usually to worn to count) persisting onto body whorl where 15-17 striae may be present above keel, and 9-10 below. Surface of shell between striae usually flat or only slightly raised. Axial sculpture consisting of fine, regular oblique axial lines of growth. Nuclear whorls about 3, smooth, light brown; first post nuclear whorl spirally sculptured. Operculum corneous, paucispiral. Periostracum not evident in specimens examined. Radula littorinid (2-1-1-1-2), similar to *L. unifasciata*; central tooth somewhat narrow.

Animal darkly pigmented on surfaces of tentacles, snout, and foot. Verge may also be darkly pigmented distally, moderately long and club shaped; having a pointed basal flap with a penial gland and a hyaline accessory flagellum; sperm duct open, deeply folded. Nothing is known concerning the reproduction and development of this species although probably it is oviparous and spawns pelagic capsules.

Measurements (mm.)—

length	width	no. whorls	locality
13.6	7.7	4+	Algoa Bay, Cape Colony
13.0	8.0	4+	"South Africa"
12.5	8.0	4+	"South Africa"
12.2	6.9	5	Algoa Bay, Cape Colony
11.8	8.1	3+	"South Africa"
10.8	6.8	4	Muizenberg, Cape Province
10.7	6.8	4+	Cape of Good Hope
9.7	6.2	4	Margate, Natal
9.6	6.6	3+	Knysna River, Cape Province
8.7	6.0	4+	Algoa Bay, Cape Colony
8.6	5.8	5	Camps Bay, Cape Colony
8.4	5.5	3	Port Elizabeth, Cape Colony
8.0	5.3	5+	Cape land betw. Port Alfred and Cape Agulhas
7.6	4.6	4	Port Alfred, Cape Colony
6.7	4.7	2+	Cape of Good Hope

Synonymy—

- 1847 *Littorina knysnaensis* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, p. 196. *Littorina* pl. 4, fig. 4, (Caput Bonae Spei ad regionem fluminis Knysna [Cape of Good Hope, South Africa, near Knysna River]); lectotype in Stuttgart Museum (NH), catalogue number MT 108: 9.3×6.0 mm. (Janus, 1961); 1848, Krauss, *Die Südafrikanischen Mollusken*, p. 102.
- 1857 *Littorina picea* Reeve, *Conchologie Iconica*, vol. 10, *Littorina*, pl. 15, fig. 83 (no locality given); lectotype BM(NH) 1968320: 6.9×4.5 mm.
- 1915 *Littorina africana tryphena* Bartsch, *United States National Museum Bulletin* 91, p. 120, pl. 38, fig. 6. (Port Alfred, South Africa); holotype USNM 187091.
- 1932 *Littorina rietensis* W. H. Turton, *the Marine Shells of Port Alfred, S. Africa*, p. 131, pl. 28, fig. 948 (Port Alfred, South Africa); type in Oxford University Museum.
- 1932 *Littorina kowiensis* W. H. Turton, *ibid.*, p. 132, pl. 28, figs. [sic] 956 (Port Alfred, South Africa); type in Oxford University Museum.
- 1932 *Littorina africana picea* 'Reeve,' W. H. Turton, *ibid.*, p. 133 [invalid emendation of *L. picea* Reeve].
- 1932 *Littorina indistincta* W. H. Turton, *ibid.*, p. 133, pl. 28, fig. 959 (Port Alfred, South Africa); type in Oxford University Museum.

Types—A lectotype for *Littorina knysnaensis* Philippi was designated by Janus (1961) from among 8 syntypes in the Stuttgart Museum MT 108. A lectotype is here designated for *Littorina picea* Reeve from among 3 syntypes in the British Museum (NH): 1968320 (see pl. 364, figs. 19, 20). The type locality for *L. picea* is here designated as South Africa. The holotype (figured specimen) of *L. africana tryphena* Bartsch is in the U.S. National Museum: USNM 187091, and the para-type originally associated with the holotype has been recatalogued: USNM 664353. The types of *Littorina rietensis*, *L. kowiensis* and *L. indistincta* all described by Turton (1932) are in the Oxford University Museum.

Records—SOUTH AFRICA: Lambert's Bay (Stephenson, et al., 1940); Saldanha Bay (ANSP); Dassen Id. (ZMA); Camps Bay (USNM); Chapman's Bay, W. of Cape Peninsula (ANSP); Muizenberg (USNM); Gordons Bay, nr. Strand, False Bay (ANSP; ZMA); Simonstown (ZMC); Simons Bay, E. Cape Point (ANSP); Cape of Good Hope (USNM); N.E. of False Bay; Buffels Bay, Cape Point; Onrust, 7 mi. W. Hermanus; Hermanus; Cape Agulhas; Cape St. Blaize, Mossell Bay (all ANSP); mouth of Knysna River, Cape Province (ex. Krauss, MCZ); Beacon Isle, Plettenberg Bay (ANSP); Sea View, 16 mi. W. of Port Elizabeth (MCZ); Beacon Point, Port Elizabeth (ANSP); Algoa Bay, Port Elizabeth, Cape Colony (MCZ; USNM); Capeland, Bushman's River mouth (USNM); Kowie R., Port Alfred (NMW); Port Alfred (ANSP; MCZ; USNM); Esplanade, East London (USNM); Coffee Bay, 1 mi. S. of Umata River; Port Edward, Natal (both ANSP); Second Beach, Port St. John, Pondoland; Margate, 11 mi. S. of Port Shepstone, Natal (both USNM).

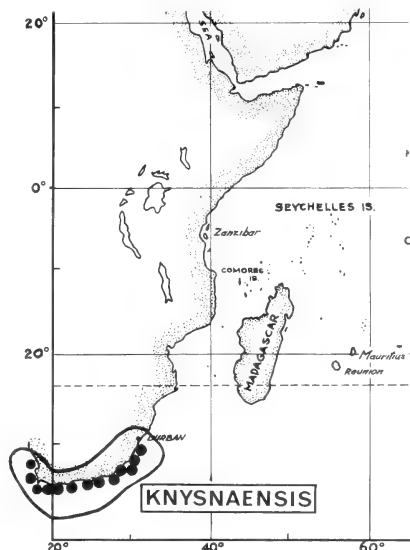


Plate 369. Geographical distribution of *Littorina (Austrolittorina) knysnaensis* (Philippi), in South Africa.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Nodilittorina von Martens, 1897

Type: *Littorina pyramidalis*

Quoy and Gaimard, 1833

Abbott (1954) pointed out that *Nodilittorina* von Martens should be considered a full genus, and designated as its type-species *L. pyramidalis* Quoy and Gaimard. He considered *Nodilittorina* to include also the west Atlantic species *L. tuberculata* Menke with somewhat similar sculpture. Habe (1956) pointed out a difference between radulae of *pyramidalis* and *tuberculata* and on that basis proposed a new subgenus for *tuberculata*, *Echinolittorina*, and at the same time suggested that *Nodilittorina* s.s. is an Indo-Pacific group. In the course of the present study, radulae have been studied of the various Indo-Pacific species thought to belong in *Nodilittorina* and all have proven close in appearance to *N. pyramidalis*.

In addition to the several Indo-Pacific species belonging to *Nodilittorina* s.s., there are a number which because of sculptural differences are here placed in the subgenus *Granulilittorina* Habe and Kosuge, 1966. One species, *N. natalensis* Philippi, because of its sculptural characters resembles *N. tuberculata*. However, its radula is not at all like *Echinolittorina* and, therefore, it is maintained in the genus *Nodilittorina* s.s.

An anatomical character apparently common to members of *Nodilittorina* is the partial separation of the penial gland from the basal enlargement of the penis. This condition differs from *Austrolittorina* where the gland is fully incorporated in the basal enlargement.

The most obvious character of *Nodilittorina*, the "nodose" sculpture, is quite apparent in the type-species, *pyramidalis*, in *natalensis* and *nodosa*. It is not always so apparent in *australis* with its highly variable sculpture. Nevertheless, because of similarities in anatomy and the apparent tendency to interbreed with *nodosa* it seems obvious that *australis* must be placed in *Nodilittorina* if current generic concepts are to be maintained.

Synonymy—

1897 *Nodilittorina* E. von Martens, in Weber's Zoologische Ergebnisse Einer Reise in Niederländisch Ost-Indien, vol. 4, pt. 1, p. 204; type-species by subsequent designation, Abbott, 1954, p. 451: *Littorina pyramidalis* Quoy and Gaimard, 1833.

Subgenus Nodilittorina von Martens, 1897

Nodilittorina pyramidalis

subspecies *pyramidalis* (Quoy and Gaimard, 1833)

(Pls. 325, 326, 370, 371)

Range—West coast of India and southeast Asia through the high islands of the Pacific to the Marquesas.

Remarks—*Nodilittorina pyramidalis* is closely related to several other species of the genus in the Indo-Pacific, eastern Pacific and western Atlantic. Present means of distinguishing these species are based largely on differences in shell characters as the various species do not differ detectably in gross anatomy. When it is possible to examine such features as comparative physiology, ecology and the morphology of chromosomes additional

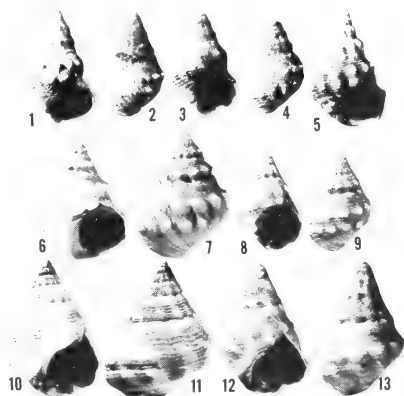


Plate 370. Figs. 1-9. *Nodilittorina pyramidalis pyramidalis*

Figs. 1,2. Holotype of *Littorina pyramidalis* Quoy and Gaimard from Jervis Bay, Australia (MHNP, 23.7 × 13.7 mm.).

Figs. 3,4. Holotype of *Littorina monilifera* Eyndoux and Souleyet, from Touranne, Cochinchina (MHNP, 11.3 × 7 mm.).

Fig. 5. Lectotype of *Littorina trochoides* Gray (BM(NH) 87.4.26.1-8, about 10 × 7 mm.).

Figs. 6,7. *Nodilittorina pyramidalis pyramidalis*, from Stradbroke Island, Queensland (USNM 684712, 18.5 × 12.8 mm.).

Figs. 8,9. The same from Koh Huyong, Similan Islands, Thailand (USNM 661209, 8.6 × 5.2 mm.).

Figs. 10-13. *Nodilittorina pyramidalis pascua* Rosewater. Figs. 10,11. Holotype (USNM 679290, 13.1 × 8.8 mm.). Figs. 12,13. Paratype (USNM 679291, 12.6 × 7.8 mm.).

Both from Easter Island, Pacific Ocean.

differences may be found. Arrangement of nodular sculpture has been found to be quite reliable in the present study: *N. pyramidalis* usually displays only two rows of white nodules on the body whorl, one at the periphery and one above it with only a single row on spire whorls (the second being covered over by the succeeding whorl); *N. natalensis* displays three rows on the body whorl, the third row, usually slightly smaller, being located at the suture, with 2-3 rows on spire whorls and with a few raised spiral sculptural cords running between the rows; *N. subnodosa* shows a similar sculptural pattern, but it is much reduced at times consisting of spiral rows of weak granulations; the subspecies of *N. pyramidalis* (see next species) inhabiting Easter Island is much like the nominate subspecies except that the two rows of nodules on the body whorl tend to coalesce producing axial bars rather than nodules, and this may be noted on the spire also; the west Atlantic species, *N. tuberculata* Menke, is like *N. natalensis* in possessing 3 rows of nodules on the body whorl and two on spire whorls. This definite difference between *N. pyramidalis* and *N. tuberculata* contradicts the statement by Abbott (1954) that the two are sibling species as they are not strictly morphologically identical. The east Pacific species *N. galapagensis* Stearns has not been collected in sufficient numbers to allow adequate understanding of its variation. The latter species with three rows of nodules on the body whorl appears more closely related to the Atlantic and east African species than to *N. pyramidalis*. Some young individuals of the east Atlantic species, *miliaris* Quoy and Gaimard, have only two main rows of nodules, but in later life develop multiple rows which causes me to place them with the members

of the subgenus *Granulilittorina* Habe and Kosuge (see world species list).

Interestingly *N. pyramidalis* is one of those species showing an affinity for high islands or continental shores as indicated by its distribution which skirts the Pacific atolls. Perhaps its preference for high shore rocks limits the species to coasts offering such a habitat.

On the coast of Queensland and New South Wales, Australia, *N. pyramidalis* apparently reaches its largest size (see measurements) and it was from this region (Jervis Bay) that the species was originally described. It is difficult to specify the reason for this gigantism, but it may possibly be related to a lack of optimal spawning temperatures or to parasitic castration either of which could prevent the onset of sexual maturity and thus prolong the active growing period.

Habitat—Usually found on shore rocks considerably above high tide line.

Description—Shell reaching 23.5 mm. (nearly 1 inch) in length; but usually less than 12 mm.; high cone or pyramidal in shape; average obesity about .63 (43 specimens ranging from .55 to .70); relatively thick in structure, imperforate, sculptured with raised spiral cords and bearing rows of raised nodules; microscopic sculpture, where not worn away or otherwise obscured, consisting of overall closely spaced wavy spiral threads. Axial sculpture consisting of oblique growth lines. External color, exclusive of nodules, dark reddish to blackish brown, nodules usually white, but sometimes a lighter reddish brown. Aperture medium to dark reddish brown, with a narrow yellowish white band revolving inward from near anterior junction of outer lip and columella; columella also medium to dark reddish brown. Base somewhat flattened; periphery nodulated. Whorls 5-6, rather flat-sided. Spire usually more than half the length of shell, produced at an angle of from 45-60°. Aperture roundly oval to nearly diamond-shaped; outer lip moderately thick; inner lip (columella) flattened, moderately excavated, especially anteriorly where a broad siphonal trough is directed at an angle of 45° to anterior-posterior axis of shell. A flattened crescent shaped area on base adjacent to columella callous. Suture distinct and covering over lower row of nodules on spire whorls. Predominant sculptural feature is double row of white nodules on body whorl, each row developing 11-15 nodules; nodules often crossed by spiral cords; one row at periphery, the second just above it; nodules usually arranged one above the other, but sometimes out of phase; a single

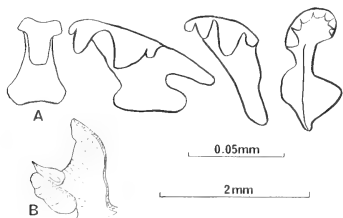


Plate 371. *Nodilittorina pyramidalis* pyramidalis Quoy and Gaimard, from Koh Phi Phi, Thailand (USNM 661502).

Fig. A. Radula (upper scale is 0.05 mm.).

Fig. B. Penis; note partial separation of penial gland from basal enlargement (lower scale is 2 mm.).

row of nodules on spire whorls; the peripheral row on spire being covered over by next succeeding whorl, but sometimes just visible above suture. Nuclear whorls worn or decoluate in all specimens examined, remaining portions smooth; postnuclear whorls nodulose. Operculum roundly oval, paucispiral. Radula littorinoid, formula 2-1-1-1-2; central tooth narrow, tricuspid; outer marginal teeth with blunt enlargements laterally.

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verges relatively short and thickened in preserved specimens, with an enlargement near its base which is partly separated from a penial gland bearing an accessory flagellum; sperm groove deeply folded; distal end of verge appears minutely papillose. Produces a pelagic capsule having 6 spiral ridges, bearing a single egg, and measuring 160 micra in diameter (Tokioka, 1950; Habe, 1956).

Measurements (mm).—

length	width	no. whorls	locality
23.5	16.4	6	Lord Howe Id.
22.5	14.2	6	Stradbroke Id., Queensland
21.8	14.5	6	Lord Howe Id.
19.3	12.1	6	Port Kembla, New South Wales
18.4	12.3	5	Sydney, NSW.
17.3	12.1	6	Stradbroke Id., Queensland
13.4	8.0	5	"Marquesas"
11.6	7.0	5+	Berhala Id., Sandakan No. Borneo
10.6	6.3	5	Pelabocan Ratoe, Java
9.7	5.9	5	Jamelo Bay, Luzon, P.I.
9.1	6.1	5	Barrow Id., betw. Cape Dupuy and Cape Malouet, W. Australia
5.4	3.0	5	Guam, Marianas

Synonymy—

- 1791 *Trochus nodulosus* Gmelin, Systema Naturae, ed. 13, vol. 1, part 6, p. 3582 (In Oceano australi, (et minor) mari; Americam meridionalem); refers to Chemnitz, Conchylien Cabinet, vol. 5, pl. 163. f. 1545, 1546; not *T. nodulosus* Solander, 1766 in G. Brander, Fossilia Hantoniensis, p. 10, pl. 6.
- 1817 *Turbo trochiformis* Dillwyn, A Descriptive Catalogue of Recent Shells, vol. 2, p. 826 (Southern Ocean); refers to Gmelin, *T. nodulosus*, p. 3582, and to Chemnitz, *ibid.*; not *T. trochiformis* Brocchi, 1814.
- 1833 *Littorina pyramidalis* Quoy and Gaimard, Voyage de L'Astrolabe, Zoologie, vol. 2, p. 482, pl. 33, figs. 12-15. (Jervis Bay [New South Wales] Australia); holotype in Paris Museum, 23.7 × 13.7 mm.; 1954, Abbott, Proceedings U.S. National Museum, vol. 103, p. 456.
- 1839 *Littorina trochoides* Gray, the Zoology of Captain Beechey's Voyage—in His Majesty's Ship *Blossom*, Mollusca, p. 140 (no locality); (lectotype, BM(NH) 87.4.26.1-8, ca. 10 × 7 mm.)

- 1846 *Littorina vilis* 'Menke' Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 145, *Littorina*, pl. 2, fig. 21 (no locality).
- 1847 *Littorina malaccana* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 3, p. 15, *Littorina*, pl. 6, fig. 17 (Pulo Pinang).
- 1851 *Littorina cecillei* Philippi, Zeitschrift für Malakozoologie, 8th Jahr, p. 78 (Ryukyu Islands).
- 1852 *Littorina monilifera* Eydouard and Souleyet, Voyage sur la Bonite, Zoologie, vol. 2, p. 559, pl. 31 figs 37-39 (Touranne, Cochinchine [Viet Nam]); holotype in Paris Museum: 11.3 × 7 mm.
- [1950] *Littorina-capsula multistriata* Tokioka, Publ. Seto Marine Biological Laboratory vol. 1, no. 3, p. 151, fig. 6, 2; non-binomial; is egg capsule of *N. pyramidalis* fide Habe, 1956; Venus, vol. 19, no. 2, p. 121.]

Types—The lectotype of *Trochus nodulosus* Gmelin and also of *T. trochiformis* Dillwyn is the specimen figured by Chemnitz which may still be extant in the Zoological Museum in Copenhagen, Denmark. Holotypes of *Littorina pyramidalis* Quoy and Gaimard and *L. monilifera* Eydouard and Souleyet are in the Paris Museum. Types of species described by Philippi: *L. vilis*, *malaccana* and *cecillei* may be in the Berlin Museum.

Nomenclature—The excellent reviews of this species by P. -H. Fischer (1967a, 1969) came to my attention when the present study was well advanced. Fischer's decision that the oldest name for this species is *N. nodulosa* (Gmelin, 1791) is correct with the unavoidable qualification that *Trochus nodulosus* Gmelin, 1791 is preoccupied by Solander in G. Brander, 1766 (see Synonymy). The next valid name, excluding *T. trochiformis* Dillwyn, 1817, also preoccupied (Brocchi, 1814) is *Littorina pyramidalis* Quoy and Gaimard, 1833. Although one may wish to clarify nomenclature by applying strictly the rules of priority, one cannot dispense entirely with the effects of homonymy. I agree otherwise almost entirely with Fischer's analysis of this species, with the exception that I have not seen records from Madagascar or the Red Sea and Persian Gulf areas and can only suggest that Fischer's records from these localities may be based on other species, such as *N. natalensis* or *subnodosa*.

Records—INDIA: Bandra, N. of Bombay (USNM); Bombay (MCZ); Vengurla, N. of Goa; Goa; Kumta (Kumta), North Kanara (all USNM); Cape Comorin; W. of Mandapam, Gulf of Mannar; Rameswaram Island, Pamban, Palk Strait; Ramen Point, W. side of Pamban Pass, betw. Gulf of Mannar and Palk Strait (all ANSP); Madras (MCZ, AMS, ANSP). CEYLON: W. of Kankasanturai (ANSP); Galle (RNHL, ANSP, USNM); Colombo (MCZ, USNM); Merissa Village (ANSP); Trincomalee (YPM). THAILAND: Ko Sindarar Nua (Chance Island); Ko Huyong (South Island), Similan Islands; Laem Phan-Pha; Ko Phuket, from around Phan-Pha point; Ko Phi Phi (all USNM); Songkhla (MCZ); Ang Thong Id.; Ko Tao; Ko Maprao; Sriracha (all USNM); Ko Nom Sao, Chanthaburi Province (MCZ); Ko Samet; Ravong, Len Sing, Len Ngob (Ngao) (all USNM). MALAYSIA: Pulau Ular, Langkai Islands (USNM); Penang (MCZ); Malacca (MCZ); Pulau Anyut, Malacca Strait, just S.E. of town of Malacca (USNM); Raffles

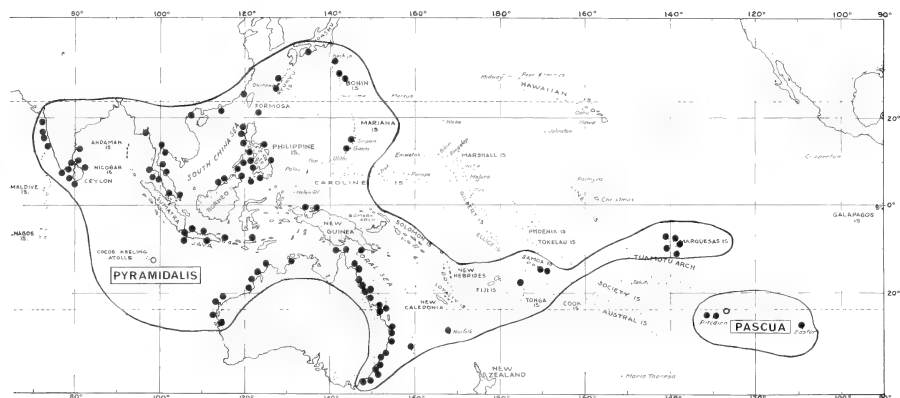


Plate 372. Geographical distribution of *Nodilittorina pyramidalis pyramidalis* (Quoy and Gaimard) and of its subspecies, *N. pyramidalis pascua* Rosewater.

Light, Singapore (ANSP, USNM); Sekudu Island, Strait of Johore (USNM). VIETNAM: Ba Lang, North Annam (USNM); Île de la Table (AMS, MCZ). CHINA: Hong Kong (ANSP, USNM); Amoy (Hsia-men); Spider Island, Foukien Province (both USNM); JAPAN: Hachioji Island, 275 mi. S. of Tokyo; Shirahama, Wakayama Pref. (both ANSP); Waki, Satsuma (BPBM). RYUKYUS: Amami Oshima (ANSP); 1 mi. N. of Shana Wan (USNM); Nago, both Okinawa (USNM, ANSP, BPBM); Zenda, Kume (MCZ, USNM, ANSP, BPBM). PHILIPPINE ISLANDS (Many localities; see map). NORTH BORNEO: Sipitang; Sulok Island, Jesselton; Berhala Island, Sandakan (all USNM); W. Marudu Bay (ANSP). INDONESIA: Pulau Sebesi, Sunda Strait; Diakarta (both RNHL); Teluk Pelabuhan Ratu (MCZ, USNM); Welkomst Bay, Bantam (USNM); Patjitan, all Java; Bali; Laranuka, Flores Island (all RNHL). COCOS-KEELING IDS.: South Id. (Maes, 1967). AUSTRALIA: QUEENSLAND: Thursday Island, (RNHL); Murray Island, both Torres Strait; No. VI Island (both AMS); No. VIII Island, both Howick Islands (ANSP); Lizard Island (AMS); Green Island (AMS, MCZ); Fitzroy Island (ANSP); Brook Island (ANSP); Palmer Islands (AMS, ANSP); Bay Rock, under clumps of dead coral and rock; Cape Cleveland nr. Townsville (both USNM); Holbourne Island, off Bowen; Hayman Island, Whitsunday Passage; Lindeman Island (all AMS); Coppersmith Island, Smith Group (USNM); Brampton Island; Coquet Island (both AMS); Yepoon; N. Keppel Island, Yepoon (both AMS, MCZ); Keppel Bay; Heron Island, Capricorn Group; Bustard Bay; Noosa Heads; Caloundra (all AMS); Point Lookout, N.E. Stradbroke Island (ANSP, AMS); Stradbroke Island (WAM). NEW SOUTH WALES: Byron Bay; Woody Head (Wooded Bluff); Budgewoi Beach; Toukley (all AMS); The Entrance (USNM); Putty Beach (AMS); Wyargine Point, Middle Harbor, Sydney (AMS); Collaroy (USNM); Long Reef, N. of Manly (ANSP); Port Jackson (ANSP, AMS, MCZ); Bottle and Glass Rocks, Sydney (ANSP); Coogee Beach, Sydney (USNM); btwn. Gratio Point and Clontarf, Sydney (AMS); La Perouse; Kurnell, both Botany Bay (both MCZ); Bird Island, off Wollongong (AMS); Port Kembla (USNM); Shellharbour (AMS); Jervis Bay (WAM, MHPN); Sussex Inlet Reef (AMS); Twofold Bay (MCZ, AMS). VICTORIA: Mallacoota (AMS). WESTERN AUSTRALIA: Point Gregory, N.W. end of Peron Peninsula, Shark Bay; below Quobba Light, N. of Carnarvon (both WAM); btwn. Cape Duprey and Cape Malouet, Barrow Island (WAM, USNM); mouth of False Cape Creek, La Grange Bay; 2 mi. S.W. of jetty, Broome; James Price Point, 35 mi. N. of Broome (all ANSP); Buccaneer Archipelago (AMS). NORTHERN

TERRITORY: Darwin (ANSP, USNM). NEW GUINEA: Manokwari; reef at S.E. entrance to Wooi Bay, Japen Island (both ANSP); Yule Island (AMS, ANSP). LORD HOWE ISLAND: (MCZ, AMS, NMW). NORFOLK ISLAND: (AMS). BONIN ISLANDS: Port Lloyd; Ani Jima (both USNM); Mukoshima (ANSP, USNM). MARIANAS: Saipan (ANSP); Apra Bay, Guam (USNM). SAMOA: Otu Island; Mutire Point; Tau; Fagamalo; Tau; Siulaga Point; Tau (all BPBM). TONGA: Nuafo'ou (BPBM). MARQUESAS: Hona Nui, Ua Huka; Hiva Oa; (both ANSP); Hanavave, Fatuhiva; Nukuhiva (both USNM, ANSP); Eiao (ANSP); Ua Pou; Tahatu (both USNM).

Nodilittorina pyramidalis

new subspecies pascua Rosewater

(Pl. 370, figs. 10-13)

Range—Oeno, Pitcairn, Henderson and Easter Islands, southeastern Pacific.

Remarks—As mentioned in connection with the nominate subspecies, the concept of *N. pyramidalis pascua* as a subspecies inhabiting the eastern-most extremities of the Indo-Pacific faunal region appears quite valid. The subspecies is distinguished primarily on the basis of its nodular sculpture. The two rows of nodules present on the whorls in *pyramidalis* s.s. have a tendency to coalesce in *pascua* forming a series of axial ridges.

The presence of *Nodilittorina pyramidalis* on Easter Island was first mentioned by Dall (1908) and it was later recorded by both Odhner (1922) and Lamy (1936) based on separate collections. None of these workers noted the differences between Easter Island populations and the species elsewhere in the Indo-Pacific.

Habitat—On rocks above high tide line.

Description—Very similar to *N. pyramidalis* with exception that the double spiral row of white nodules is replaced by a row of axial bars (resulting from coalition of juxtaposed nodules). Reaching 15.3 mm. in length (about .6 inch); average obesity about .64 (22 specimens range from .57 to .69). Usually only one row of small nodules on base. Axial bars on spire whorls half covered by undulating suture. Color more uniform than in *pyramidalis*; generally overall bluish gray, axial bars occasionally white or a dark brown; aperture very dark brown, with a dark brown flattened crescent shaped area on base adjacent to and parallel with columella. Nuclear whorls about 2, medium brown, smooth, shining; postnuclear whorls with axial sculpture. Radula and anatomy generally similar to *N. pyramidalis pyramidalis*.

Measurements (mm.)—

length	width	no. whorls	locality
15.3	9.8	7+	All Easter Island
14.5	8.3	5+	Paratype
14.0	8.7	6+	Paratype
13.7	8.6	5+	Paratype
13.1	8.8	7	Holotype
12.8	8.2	7+	Paratype
12.3	7.8	6+	Paratype
10.1	6.2	6+	Paratype
9.3	5.8	6+	Paratype
8.9	5.3	6+	Paratype

Types—The holotype of *Nodilittorina pyramidalis pascua* (a female; USNM 679290) and 24 paratypes (males and females; USNM 679291) were collected in October, 1968, on Easter Island by Pat McCoy. Additional paratypes from the same source are in the Academy of Natural Sciences, Philadelphia. The latin word *pascua*, meaning "Easter" is used in the combination *N. pyramidalis pascua* as a noun in apposition.

Records—Oeno Island (USNM); Pitcairn Island (BPBM; USNM); Henderson Island (Smith, 1913); Easter Island (USNM; ANSP).

Nodilittorina australis (Gray, 1826)

(Pls. 325, 373)

Range—Western Australia, from Esperance to Vansittart Bay.

Remarks—*Nodilittorina australis* is endemic to Western Australia. It is closely related to another endemic species, *Nodilittorina nodosa* Gray, with which it is found in at least part of its range living in what appears to be the same or a very similar ecologic niche on rocks low in the intertidal zone. Comparison of gross anatomies and radulae show no outstanding differences although the shells of

the two species are clearly distinct. Specimens showing characters intermediate between *N. australis* and *nodosa* found in the same population with these species are judged to be hybrids (pl. 373, figs. 11-16). The observed similarities in the anatomy of reproductive organs are believed to permit successful inter-species copulation and hybridization, although this phenomenon has not been recognized often in Mollusca (see Boss, 1964). Hybrid specimens *N. australis* × *N. nodosa* are fairly easily recognizable. They are on the average more slender than either parent (.66 obesity versus .68) tend to show more typically *nodosa* shell characters during early growth, but in later growth take on more the appearance of *australis*.

True *australis* may be recognized by its rather globose shell, generally rough but not nodose sculpture which is often wrinkled axially, light tan to light violet colored aperture which has a relatively broad white band revolving within it. Spire sculpture is granulose but never nodulose. In comparison, the shell of *nodosa* is pyramidal with two rows of large whitish to orange nodules, one row at the suture and one at the periphery of the body whorl; on spire whorls there is one row at the uppermost extremity and one at the lowermost. Coloration of *nodosa* is dark brown, especially within the aperture, with a relatively narrow revolving white band at its lower extremity. The shape of aperture in *australis* is roundly oval, while in *nodosa* it is nearly diamond shaped. Related to the shape of aperture is the presence of a nodose keel in *nodosa* and the virtual absence of a keel in *australis*. Hybrid individuals exhibit a variety of characters generally intermediate between *australis* and *nodosa*.

Habitat—On rocks of the lower splash zone, intertidal.

Description—Shell reaching 23.4 mm. (about 0.9 inch) in length, subglobose to subtruncate in shape, average obesity about .68 (28 specimens range from .63 to .75); relatively thick in structure, imperforate, usually developing a flattened, crescent-shaped area adjacent to columellar callous; sculptured with rather heavy spiral cords and often pronounced axial growth wrinkles. External color grayish to yellowish white. Aperture light yellowish tan to light violet, with a broad white band near anterior junction of outer lip and columella. Base hardly flattened with only a very low keeling effect at periphery. Whorls 4-6, moderately well rounded, especially the body whorl. Spire less than half the length of shell, convex,

produced at an angle of about 75°. Aperture oval; outer lip moderately thick, inner lip concave, thickened. Columella usually light violet to tan, hardly excavated but with a flattened crescent-shaped area on the adjacent base. Anterior junction of outer lip and columella projecting to form a weak siphonal channel which occasionally bears a series of very fine linear scratches. Suture not deeply impressed. Spiral sculpture varying from simple to moderately granulose, consisting of from 5-8 raised spiral cords on spire whorls and 18-20 on the body whorl; sculpture often thrown into axial wrinkles by growth pattern, either in part or over entire surface of shell—giving a reticulated appearance. Entire surface covered with closely spaced, fine, wavy, spiral threads, most noticeable in grooves between spiral cords; not detectable in worn specimens. Ir-

regular, fine axial growth lines also present. Operculum corneous, only moderately thick, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls about 3 in number, light tan in color, smooth; first post-nuclear whorls similarly colored but spirally sculptured, becoming rapidly granulose. Radula littorinid (2-1-1-1-2) central tooth very narrow (much like *N. pyramidalis*).

Animal darkly pigmented on surfaces of tentacles, snout and foot. Verge moderately short and thick, yellowish white in color; having a bipartite (mitten-shaped) basal flap the "thumb" appendage bearing a penial gland having a hyaline accessory flagellum (similar to *N. pyramidalis*). Nothing is known concerning reproduction and development of this species, although it probably is oviparous and spawns pelagic capsule.

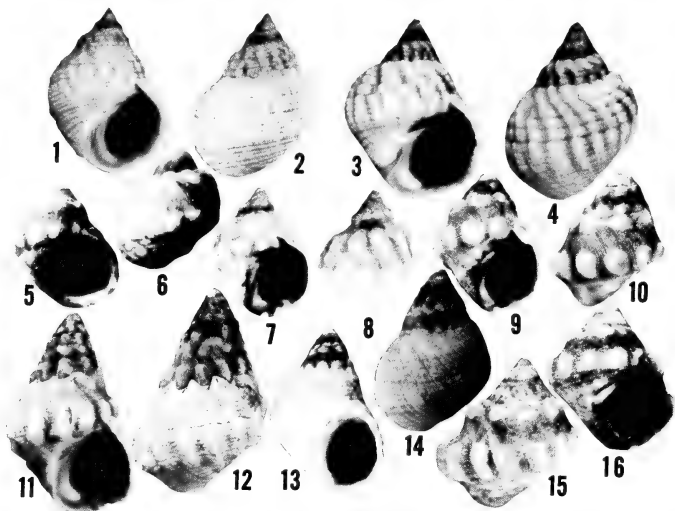


Plate 373. Figs. 1-4, *Nodilittorina australis* (Gray, 1826).

Figs. 1,2. Neotype of *Littorina australis* Gray, from South Mole, Fremantle, Western Australia (WAM 292-70, 15.1 × 11 mm.).

Figs. 3,4. An especially "rugose" specimen from Port Denison, Western Australia (USNM 691677, 12.3 × 8.1 mm.).

Figs. 5-10. *Nodilittorina nodosa* (Gray, 1839).

Figs. 5,6. Lectotype, from north coast of Western Australia (BM(NH) 87.4.26.10-12; 10.1 × 7.3 mm.).

Figs. 7,8. Specimen from Red Bluff, Kalbarri, near mouth of Murchison River, Western Australia (USNM 691680, 13 × 8.9 mm.).

Figs. 9,10. A young specimen from the same locality (7.5 × 5.2 mm.).

Figs. 11-16. Supposed *N. australis* × *nodosa* hybrids; note early "nodose" sculpture becoming more like *australis* in figs. 11-14.

Figs. 11,12. from Vansittart Bay, northern Western Australia (USNM 684714, 17.7 × 10.7 mm.).

Figs. 13,14. from Port Denison, Western Australia (USNM 691678, 14.4 × 9.2 mm.).

Figs. 15,16. Specimen from same locality as figs. 7-10, possibly a young hybrid; note elongated nodules (8.2 × 5.7 mm.).

Measurements (mm.)—

length	width	no. whorls	locality
23.4	17.6	4+	"Australia"
19.0	12.4	6	All Red Bluff, Kalbarri, West Australia
18.0	12.0	6	
17.5	11.0	5+	
16.2	10.2	6	
16.0	11.3	4+	
15.3	11.0	5+	
15.1	10.2	5+	
14.7	10.1	5+	
13.8	9.5	5+	
13.5	9.4	6	
12.5	9.2	5+	
11.5	7.7	5+	
10.7	7.1	5	

Synonymy—

1826 *Littorina australis* J. E. Gray in P. P. King, Narrative of a Survey of the Intertropical and Western coasts of Australia, vol. 2, Appendix B, p. 483 (type locality here designated, South Mole [Arthur's Head] mouth of Swan River Fremantle, Western Australia.) Neotype designated here; West Aust. Mus. 292-70; not *Littorina australis* Gray, 1839, a *Risella*.

1843 *Littorina rugosa* Menke, Molluscorum Novae Hollandiae Specimen pg. 9 (ad scopulos calcareos collis Arthurshead, od ostium fluvii cygnorum [mouth of Swan River, Fremantle, Australia]); 1844, Zeitschrift für Malakozoologie, Jahrgang 1844, p. 57 [synonymizes *L. rugosa* with *L. australis* Gray, 1826].

Types—According to the notes given by Gray (1826, *ibid.*, p. 496) specimens of *L. australis* were not among the species deposited by him in the British Museum collections, nor were representatives of this species found there during my recent search for types of Littorinidae. It is fairly certain, therefore, that type-specimens of this species and also that of its only other synonym, *L. rugosa* Menke, may be considered lost. In order to stabilize the concept of the species I consider it necessary to designate a neotype (I.C.Z.N., Art. 75, 1961).

Neotype designation—Specimens of *Littorina australis* Gray, 1826, were collected from rocks at South Mole [Arthur's Head], at the mouth of the Swan River, Fremantle, Western Australia, by B. R. Wilson and A. Paterson, February 9, 1968. This is a locality from which specimens could have been collected during Captain King's survey and it is here designated the type-locality for *L. australis*. It is also the type-locality of *L. rugosa* Menke. The specimen designated as neotype of *L. australis* Gray, 1826, is catalogued as Western Australian Museum 292-70 and is figured in pl. 373, figs. 1, 2. Additional specimens from the neotype lot are catalogued as U.S.N.M. 679292. Measurements of Neotype: length 15.1 mm.; width 11.0 mm.

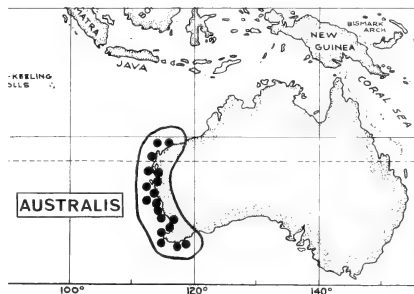


Plate 374. Geographical distribution of *Nodilittorina australis* (Gray), in Western Australia.

Records—AUSTRALIA: WESTERN AUSTRALIA: Esperance (Hodgkin et al. 1966); Middleton Beach, nr. Albany (WAM); Foul Bay (AMS); Margaret River (WAM); Augusta (NMW); Yallingup, Cape Naturaliste (USNM, WAM); Geographe Bay; Cottesloe (both AMS); Cockburn Sound (WAM); Rottnest Island (WAM, AMS); Garden Island, S.W. of Fremantle (WAM); Fremantle (USNM); Snag Island; Beagle Islands (both WAM); Port Denison (USNM, WAM); Irwin River (AMS); Abrolhos Islands (WAM); Pelsart Islands; Geelvink Chain, W. of Geraldton (AMS); Rat Island (WAM); Shark Bay, Freycinet Estuary, Eagle Bluff; Denham, Shark Bay, Peron Peninsula; S.E. Dirk Hartog Island (all WAM); Dirk Hartog Island, Shark Bay (AMS); below Quobba Light, Blow Holes, N. of Carnarvon (WAM); Red Bluff, Kalbarri, nr. mouth of the Murchison River (USNM, WAM); Point Cloates, nr. Ningaloo (AMS); Mouth of Bigota Creek, Barrow Island; btwn. Cape Dupuy and Cape Malouet, Barrow Island, (both USNM, WAM); Vansittart Bay (USNM, AMS).

Nodilittorina nodosa (Gray, 1839)

(Pls. 325, 373)

Range—Western Australia, from the vicinity of Geraldton northward [based on available records].

Remarks—The failure of this species to appear often in collections outside of Australian Museums is probably due in large part to its limited distribution in Western Australia. It is also readily confused with *N. australis* because the two species apparently hybridize and the hybrid forms look like intermediates of a variational continuum. The species is here considered to be distinct although closely related to *australis*. It may be recognized readily by its characteristic diamond shaped outline and the two rows of rather large whitish to reddish brown nodules on the body whorl. See remarks under *N. australis*.

Habitat—On rocks of the splash zone, intertidal, usually occurs with *N. australis* Gray.

Description—Shell reaching 13.3 mm. (about 0.5 inch) in length, with a diamond-shaped outline, average obesity about .68 (29 specimens range from .64 to .72); moderately thick in structure, imperforate, usually developing a flattened crescent-shaped area adjacent to columellar callosus; with two rows of whitish to reddish brown nodules on spire and body whorls. External color very dark-brown between nodules. Aperture very dark-brown with a relatively narrow white band near anterior junction of outer lip and columella; white spots on inner edge of outer lip mark inner side of last nodules; columella usually lighter brown than interior of aperture. Base somewhat flattened, the effect accentuated by the large row of nodules at periphery. Whorls 4-5, rather flat-sided. Spire usually eroded, considerably less than half the length of shell, convex, produced at an angle of about 66°. Aperture diamond-shaped; outer lip moderately thick; inner lip concave, thickened. Columella usually light-brown to light-violet, very shallowly excavated, with a flattened crescent-shaped area distally on the adjacent base. Anterior junction of outer lip and columella project forming weak siphonal channel which together with inner edge of outer lip occasionally bear series of very fine linear scratches. Suture not deeply impressed, but undulating around nodules of preceding whorl. Spiral sculpture of body whorl consisting of 2 rows, each containing about 9 large nodules arranged at the suture and periphery; penultimate whorl with about 11 nodules in each of 2 rows at either suture, the anterior row partly covered over by the body whorl. Other spiral sculpture consisting of rather low cords interspersed with fine wavy white spiral threads. Axial sculpture consisting of fine irregular growth lines and crevices resulting

from injury repair. Operculum corneous, rather thin, paucispiral. Periostracum not evident in specimens examined. Nuclear whorls eroded in all specimens examined. Radula littorinid (2-1-1-1-2) central tooth extremely narrow. Anatomy of animal similar to that of *N. australis*.

Measurements (mm.)—

length	width	no. whorls	locality
13.3	8.8	4+	All Red Bluff, Kalbarri, Western Australia
12.5	8.4	3+	
11.6	7.3	3+	
10.9	7.2	4	
10.0	6.5	3+	
9.8	6.8	3+	
8.8	5.9	4+	
8.3	5.8	4+	
6.4	4.4	3+	
6.4	4.6	3+	

Synonymy—

1839 *Littorina nodosa* Gray, the Zoology of Captain Beechey's Voyage—in His Majesty's Ship *Blossom*, Mollusca, p. 139 (no locality given; not figured [type locality here designated: North coast of Western Australia]); lectotype in British Museum (N. H.) 87.4.26.10-12; 10.1 × 7.3 mm. 1847, Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, p. 160, pl. 3, fig. 7.

Types—The lectotype of *Littorina nodosa* Gray, here designated, is in the British Museum (NH) (see pl. 373, figs. 5, 6). It bears BM(NH) catalogue number: 87.4.26.10-12; there are 2 paralectotypes under the same number. Measurements of the lectotype are 10.1 × 7.3 mm.

Records—WESTERN AUSTRALIA: Port Denison (WAM; USNM); North Island, Abrolhos Islands (WAM); Red Bluff, Kalbarri (WAM; USNM); Quobba Point, 40 miles N. of Carnarvon (ANSP; USNM); Northwest Cape (AMS); Vansittart Bay (AMS; USNM).

[*Nodilittorina australis* × *N. nodosa* hybrids]

(Pl. 373, figs. 11-16)

Range—Coextensive with *N. australis* and *N. nodosa*.

Remarks—See remarks under *N. australis*. In shell characters hybrids appear intermediate between *australis* and *nodosa*. Their average shell obesity is less than either parent: .66 compared with about .68 (23 specimens range from .61-.72). Gross anatomy of the two species is similar and hybrids show no marked differences. Laboratory and field studies should be carried out to determine whether introgressive hybridization is taking place and other details of this phenomenon.

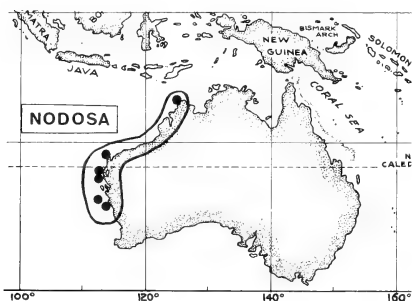


Plate 375. Geographical distribution of *Nodilittorina nodosa* (Gray), in Western Australia.

Habitat—On rocks of the splash zone, intertidal.

Measurements (mm.)—

length	width	no whorls	locality
18.8	11.8	5	Port Dennison
18.2	11.6	4+	All Red Bluff, Kalbarri, W. Australia
17.6	11.6	4+(eroded)	
16.4	10.8	4+	
15.8	10.5	4+	
15.0	9.2	5+	
14.4	9.8	4+	
13.5	8.9	4+	
13.0	9.2	3+	
12.9	8.8	4+	
12.0	8.7	3+	

Synonymy—So far as can be determined no scientific names have been established for these hybrid forms. The combination *N. rugosa* × *N. nodosa* has no validity or standing in zoological nomenclature.

Nodilittorina natalensis (Philippi, 1847)

(Pl. 376, fig. 1-6)

Range—East Africa and Madagascar.

Remarks—*Nodilittorina natalensis* has a rather narrow range in East Africa and the southwestern Indian Ocean. It is replaced in south Asia and the remainder of the Indo-Pacific by another somewhat similar appearing *Nodilittorina*, *N. pyramidalis*. However, it may readily be distinguished by the appearance of the nodular sculpture: *natalensis* usually having at least three major spiral rows of white nodules on the body whorl and 2 or 3 rows on the spire whorls, while *pyramidalis* has two rows on the body whorl and one on the spire whorls; *natalensis* also usually has a medium- to light-brown spire apex, whereas the apex of *pyramidalis* is either eroded or not noticeably different in color from the rest of the shell. In sculpture *natalensis* is closer in appearance to the west Atlantic *N. (Echinolittorina) tuberculata* than to any Indo-Pacific species. The similarity does not extend to the radula, however, that of *natalensis* being much better developed than that of *tuberculata* whose radula appears to have suffered reduction in the numbers of cusps on the lateral and marginal teeth and in the width of the central.

Habitat—Shore rocks above the splash zone.

Description—Shell reaching 14.5 mm. (about .6 inches) in length, pyramidal in shape; average obesity about .64 (32 specimens range from .59 to .69); relatively thick in structure, imperforate,

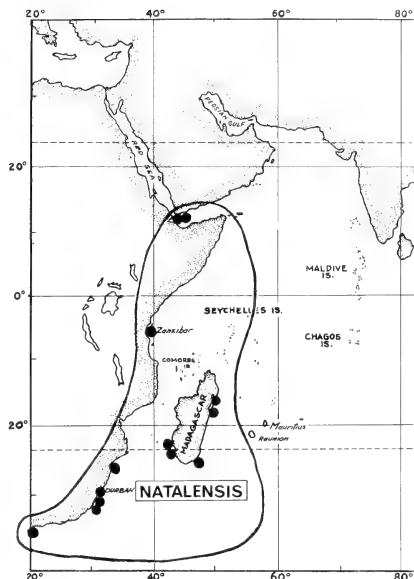


Plate 377. Geographical distribution of *Nodilittorina natalensis* (Philippi), in the western Indian Ocean.

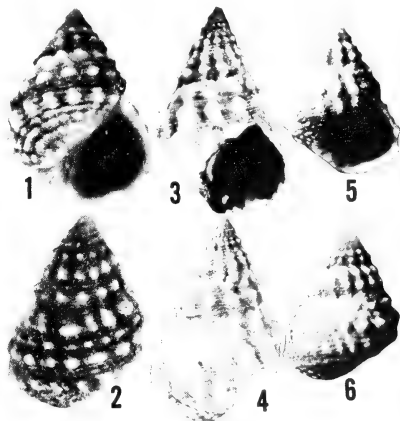


Plate 376. *Nodilittorina (Nodilittorina) natalensis* (Philippi, 1847). Note 3 rows of nodules at and above periphery.

Figs. 1, 2. Lectotype, from Coast of Natal, South Africa (Stuttgart Museum (NH): MT 109, 12.2 × 8.5 mm.; photo from Janus, 1961, Stuttgarter Beiträge zur Naturkunde, no. 70, pl. 3, figs. 7, 8).

Figs. 3, 4. Specimen from Point Ibanona, Fort Dauphin, southeast Madagascar (USNM 679281, 13.1 × 7.7 mm.).

Figs. 5, 6. Possible paralectotypes "ex Krause", from Natal (Senckenberg Museum, 11.5 × 7.9 mm.).

sculptured with raised spiral cords and bearing rows of raised nodules; microscopic sculpture, where not worn away or obscured, consisting of overall, closely-spaced spiral threads. Axial sculpture consisting of fine lines of growth. External color, exclusive of nodules and apex, dark blackish brown; nodules usually grayish to yellowish white. Aperture medium to dark reddish brown, with a narrow white band revolving inward from near anterior junction of outer lip and columella, in some specimens there is a wider light colored band near posterior junction of outer lip and columella. Apex light to medium brown. Base flattened with nodulose cords. Whorls 5-7, very slightly rounded. Spire usually more than half the length of shell, occasionally nearly coequal with length of aperture, produced at an angle of from 53-64°. Aperture roundly oval—subquadrate; outer lip moderately thick; inner lip (columella) moderately flattened and excavated, especially anteriorly where a broad siphonal trough is directed at an angle of 45° to anterior-posterior axis of shell; a flattened, crescent-shaped area on base adjacent to columella callous. Suture rather indistinct. Predominant sculptural feature: three rows of white nodules on body whorl, each row developing 13-15 nodules often crossed by spiral cords; one row at periphery, the second just above it, the third just below suture; nodules usually arranged one above the other, but sometimes out of phase; occasionally one or two accessory nodulated rows may develop from spiral cords between primary rows, especially high on whorl. Two to three nodule rows appear on spire whorls. Spiral cords on base often moderately nodulose. In an exceedingly well-preserved specimen from Chango Island, Zanzibar (ANSP) with nuclear whorls intact, the latter consist of about two smooth, light brown volutions; first postnuclear whorl also smooth, but succeeding whorls spirally striate and becoming nodulose. Operculum thin, chitinous, light-brown, oval, paucispiral. Radula littorinid, formula 2-1-1-1-2; central tooth very narrow, tricuspid, the outer cusps held high above center cusp and close to body of tooth.

Animal darkly pigmented on anterior upper surface of head, and also tentacles, snout and foot. Verge relatively short and thick in preserved specimens, with an enlargement near its base which is partly separated from a penial gland bearing an accessory flagellum; sperm groove deeply folded. Reproduction unknown; probably oviparous, producing pelagic capsule.

Measurements (mm.)—

length	width	no. whorls	locality
14.3	9.1	6+	Fort Dauphin, Madagascar
13.7	8.4	6+	Fort Dauphin, Madagascar
13.2	7.8	7+	Fort Dauphin, Madagascar
12.2	7.3	7+	Fort Dauphin, Madagascar
11.7	7.2	6+	Coast of Natal (ex Krauss)
10.5	7.1	6+	Coast of Natal (ex Krauss)
9.6	5.9	6+	Faty, Madagascar
8.9	6.1	6+	Coast of Natal (ex Krauss)
8.3	4.9	7+	Faty, Madagascar
7.4	4.9	6+	Coast of Natal (ex Krauss)
6.8	4.5	7	Inhaca Island, Mozambique

Synonymy—

1847 *Littorina natalensis* Philippi, *Abbildungen und Beschreibungen Conchylien* vol. 2, p. 160. *Littorina* pl. 3, fig. 4. (Coast of Natal, South Africa); lectotype in Stuttgart Museum, MT 109: 12.2 × 8.5 mm. (Janus, 1961): 1848 Krauss, *Die Sudafrikanischen Mollusken*, p. 102.

Types—Janus (1961) designated a lectotype for *L. natalensis* Philippi from specimens collected by Krauss and deposited in the Staatlichen Museum für Naturkunde in Stuttgart (pl. 376 figs. 1, 2).

Records—SOUTH AFRICA: Cape of Good Hope (ANSP): Second Beach, Port Saint Johns, Pondoland; Margate, 11 mi. S. of Port Shepstone, Natal; Port Edward, Natal; Tiger Rocks, Isipingo, Natal (all ANSP); Durban, Natal; mouth of the Umhlali River, Natal (both MCZ). MOZAMBIQUE: Inhaca Island, Delagoa Bay, (USNM, ANSP). TANZANIA: Chango (Prison) Island, W. Zanzibar (ANSP). ADEN PROTECTORATE: Conquest Bay (USNM). MADAGASCAR: Faty (Ihatz), 13 mi. N. of Tulear; Anako, 20½ mi. S. of Tulear; Pointe Ibañona, Port Dauphin; Flacourt, Fort Dauphin; S.W. shore Ile aux Nates, S. of Ile Ste. Marie; 2.5 mi. N.E. of Pointe D'Antsiraikiraiky, N.W. Ile Ste. Marie (all MCZ).

Subgenus *Granulilittorina*

Habe and Kosuge, 1966

Type: *Granulilittorina millegrana* (Philippi, 1848)

The subgenus *Granulilittorina* forms a convenient group for those rather globose *Nodilittorina* having multiple rows of low granular sculpture as contrasted with the members of *Nodilittorina* s.s. which are more pyramidal in shape and usually exhibit only one to three rows of larger nodules. The radulae and other anatomical details appear grossly similar in the two subgenera.

Synonymy—

1966 *Granulilittorina* Habe and Kosuge, *Shells of the World in Colour*, vol. 2, *The Tropical Pacific*, p. 20, pl. 6, fig. 13; *Venus*, vol. 24, no. 4, pp. 313, 328; type-species by monotypy *Granulilittorina philippiana* Habe and Kosuge, 1966 [= *Nodilittorina* (*Granulilittorina*) *millegrana* (Philippi, 1848)].

Nodilittorina millegrana (Philippi, 1848)

(Pls. 326, 378, 379, 380)

Range—From the Red Sea and western Indian Ocean islands to the western Pacific where it occurs sporadically as far east as the Marshall Islands.

Remarks—Better known by several of its synonyms *L. millegrana* is an extremely variable species throughout its range in the Indo-Pacific. Much of the variation may be ecologically influenced. A form exhibiting reticulate sculpture, possibly representing the doubtful species *L. reticulata* Anton, occurs on Indian Ocean Islands and in the Pacific has been found sporadically in the Philippines, and as far eastward as Eniwetok, Marshall islands, apparently showing a preference for islands. Axially and spirally striped color forms occur more or less randomly throughout the species range, but perhaps appear more commonly in the Philippines, East Indies and Australia. Variation in shell granulation is consider-

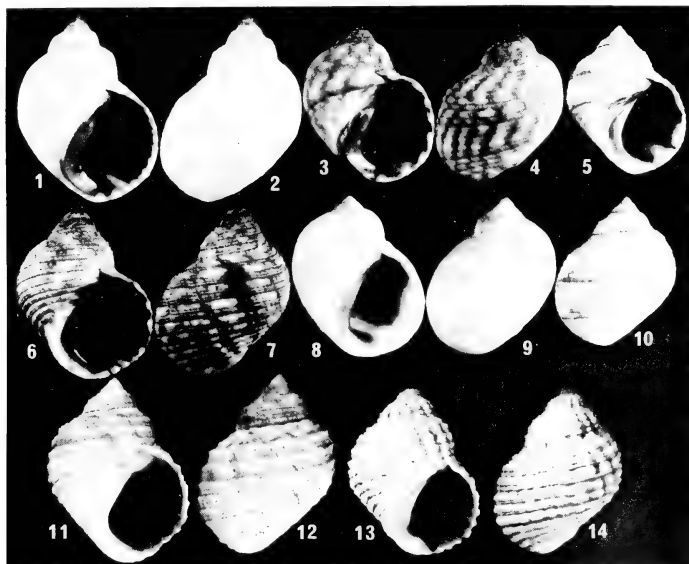


Plate 378. *Nodilittorina* (*Granulilittorina*) *millegrana* (Philippi, 1848), showing shell variations.

Figs. 1,2. Noumea, New Caledonia (USNM 679730, 11.8 × 7.6 mm.).

Figs. 3,4. Near Jesselton, North Borneo (USNM 658369, 8.0 × 5.3 mm.).

Figs. 5,10. Barrow Id., Western Australia (USNM 691690, 9.2 × 6.4 mm.).

Figs. 6,7. Tsutsu, Tsushima Id., Nagasaki, Japan (USNM 679181, 8.7 × 5.5 mm.).

Figs. 8,9. Point de Galle, southwest Ceylon (USNM 672392, 12.2 × 8.5 mm.).

Figs. 11,12. Goa, India (USNM 442974, 10 × 6.7 mm.).

Figs. 13,14. Eniwetok Id., Eniwetok Atoll, Marshall Ids. (USNM 679731, 9.3 × 6.2 mm.).

able. Its limits are at present considered to include forms ranging from smooth to rather heavily granulose. Constant characters include the generally globose appearance, the fact that the aperture is usually more than half the length of shell and the more or less dependable presence of some degree of granulation. This is the *Littorina granularis* "Gray of authors" (non Gray). As shown by Yen (1942), the species *granularis* has as its type an Atlantic specimen and is probably synonymous with *N. miliaris* (Quoy and Gaimard) from the Eastern Atlantic, rather than *Tectarius muricatus* (Linné) as suggested by Yen (see pl. 325).

Habitat—On shore rocks above high tide line.

Description—Shell reaching 13.7 mm. (about 0.5 inch) in length, subglobose to subtruncate in shape; average obesity about .67 (56 specimens range from .59 to .76); moderately thick in structure, imperforate; surface occasionally smooth, but more often bearing raised, granulose spiral cords on spire and body whorls; overall microscopic sculpture where not worn away or otherwise obscured consisting of many fine wavy spiral threads most easily observable between primary granulose spiral cords. Axial sculpture usually limited to irregular axial lines of growth, occasionally, especially in island populations, granulations are in phase axially and reticulate appearance results. External color variable, ranging from overall grayish white to spotted and axially and spirally striped with yellow to reddish brown markings. Aperture medium to dark brown, often the former lighter color with stripes or spots of the darker color, usually with a white band revolving inward from near anterior junction of outer lip and columella; columella also medium to dark brown. Base not greatly flattened; periphery not markedly differing in its contour from rest of body whorl. Whorls 5-7, well-rounded. Spire usually less than half the length of shell, produced at an angle of from about 68-73°. Aperture widely oval; outer lip moderately thick, occasionally slightly flaring, inner lip (columella) strongly developed, broad, thick, occasionally bulging posteriorly, shallowly excavated; with a flattened crescent shaped area on base adjacent to columella callous, at times approaching a columella chink. Suture well impressed. Predominant sculptural feature, 9-10 spiral cords bearing granulations on body whorl and 4-5 cords on spire whorls; granulation-bearing cords usually interspersed with non bearing cords, the latter often weaker; granulations

often subdued and some shells virtually smooth. Nuclear whorls brown to black, smooth and shining; postnuclear whorls becoming rapidly granulose and usually having a single dark spiral color band. Operculum paucispiral, brown, oval. Radula littorinid, formula 2-1-1-1-2; central tooth only moderately narrow, tricuspid.

Animal darkly pigmented on upper surface of tentacle, snout and foot. Verge long and slender, with an enlargement near its base partly separated from a penial gland containing an accessory flagellum; sperm groove deeply folded. Produces a pelagic egg capsule, having 3 tiers and an undulate border (see Tokioka and Habe, 1953.)

Measurements (mm.)—

length	width	no. whorls	locality
13.7	9.2	5	Goa, India
13.7	8.1	5	Bombay, India
12.3	8.6	4+	Pt. de Galle, Ceylon
11.3	7.3	5	Pondicherry, India
10.7	7.2	4	Goa, India
9.7	6.3	5	Koh Phi Phi, Thailand
8.4	5.4	6	Souillac, Mauritius
8.1	5.6	5	Hong Kong
7.8	5.4	4	Barrow Island, Western Australia
6.7	4.2	4	Réunion
5.9	4.5	5	Keppel Bay, Queensland
5.5	3.6	4	Koh Huyong, Thailand

Synonymy—

- Littorina granularis* 'Gray' of Authors, non Gray, 1839 [Gray's holotype, BM(NH) 87.4.26.9 is an eastern Atlantic species, *Nodilittorina miliaris* (Quoy and Gaimard)].
- 1847 *Littorina picta marmorata* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, p. 167, pl. 3, fig. 26 [lectotype figure] (provincia Illocos borealis insulae Luzon); not *L. marmorata* Pfeiffer, 1839.
- 1847 (Sept.) *Littorina ventricosa* Philippi, *ibid.*, vol. 3, *Littorina* p. 51, pl. 6, fig. 19 [lectotype figure] (Pulo Pinang [Penang Island, Malaysia]); not *L. scabra ventricosa* Philippi, 1847 (April).
- 1848 *Littorina millegrana* Philippi, *ibid.*, p. 65, pl. 7, fig. 15 [lectotype figure] (Red Sea), original measurements about 13 × 11 mm.
- 1852 *Littorina radiata* Eyndoux and Souleyet, *Voyage sur la Bonite*, vol. 2, p. 562, pl. 31 figs. 46, 47 (Touranne, Cochinchine [Viet Nam]); lectotype BM(NH) 54.7.24.389, 11.5 × 7.6 mm.
- 1857 *Littorina novaezelandiae* Reeve, *Conchologia Iconica*, vol. 10, *Littorina* pl. 14, fig. 74 (New Zealand [Trincomali, Ceylon, here corrected]); lectotype BM(NH) 1966.124, 13.2 × 9.0 mm. designated by Biggs, 1966, *Journal of Conchology*, vol. 26, no. 2, p. 138, pl. 7, fig. 5.
- 1857 *Littorina granocostata* Reeve, *ibid.*, pl. 15, fig. 79 (Brisbane Water [New South Wales] Australia); lectotype BM(NH) 1968.318, 6.3 × 4.4 mm.
- ?1859 *Littorina vidua* Gould, *Proceedings of the Boston Society of Natural History*, vol. 7, p. 138, (Ousima [= Amami-o-shima, Ryukyu Islands, according to Johnson, 1964]); type lost.

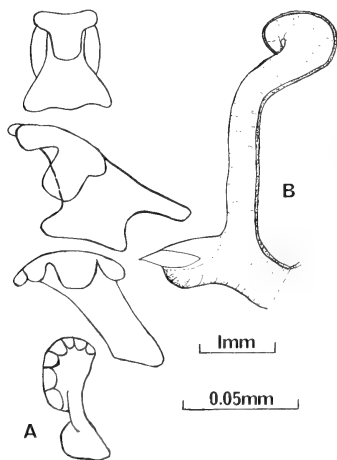


Plate 379. *Nodilittorina* (*Granulilittorina*) *millegrana* (Philippi, 1848).

Fig. A. Radula of specimen from Aden (USNM 679341; lower scale is 0.05 mm.).

Fig. B. Penis of specimen from Sekudu Id, near Singapore, Malaysia (USNM 660756; upper scale is 1 mm.).

- 1876 *Littorina melanacme* E. A. Smith, Journal of the Linnean Society of London, Zoology, vol. 12, p. 552, pl. 30, fig. 21 (San Christoval, Solomon Islands); Holotype BM(NH) 76.1.10.67, 9.6 × 6.1 mm.
- 1885 *Littorina erronea* Nevill, Hand List of Mollusca in the Indian Museum, part 2, p. 152 (Balapiti, Ceylon); new name for *Littorina novaezelandiae* Reeve, 1857.
- 1887 *Littorina granicostata* E. A. Smith, Proceedings of the Zoological Society of London for 1887, part 3, p. 519, fig. 2, (Christmas Island, Indian Ocean); Holotype BM(NH) 1968358, 10.4 × 7.2 mm.; is *Littorina insularis* E. A. Smith, 1889.
- 1889 *Littorina insularis* E. A. Smith, Proceedings of the Zoological Society of London for 1888, part 4, p. 536; new name for *L. granicostata* E. A. Smith, 1887.
- 1897 *Littorina ventricosa strubelli* von Martens, Zoologische Ergebnisse Einer Reise in Niederländisch Ost-Indien, vol. 4, part 1, p. 208 (Krakatau, Indonesia); type in Zoological Museum Amsterdam?; refers to *L. pusilla*, and to Philippi, "Abbild. Neuer Conch. vol. 2, p. 164, pl. 4, fig 15 [pl. 3, fig 23?]; and to Kuster, Conchylien-Cabinet, vol. 2, pt. 9, p. 11, p. 1 fig. 20-22; 1925 Jutting, Treubia Batavia, vol. 6, p. 142 [not a new variety of Jutting's as indicated by H. B. Preston, Zoological Record, vol. 62, Mollusca, p. 54].
- 1915 *Littorina eudeli* Sowerby, Annals and Magazine of Natural History, series 8, vol. 16, No. 93, p. 167, pl. 10, fig 5 (Pondicherry, India); holotype BM(NH) 1919, 12.31.33, 12 × 7.4 mm. *L. e. L.*
- 1936 *Littorina chaoi* T-c Yen, Notes de Malacologie chinoise, vol. 1, fas. 3, Musee Heude, Shanghai, p. 3 (Pok-hoy [Gulf of Tonkin] China); 1937, *ibid.*, fas. 4, figs 2, 2a, 2b; holotype in Museum Heude?

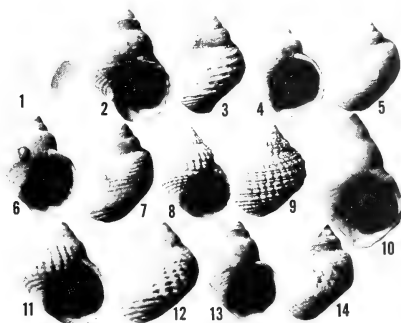


Plate 380. Type specimens of synonyms of *Nodilittorina* (*Granulilittorina*) *millegrana* Philippi, 1848).

Fig. 1. Lectotype figure of *Littorina millegrana* Philippi, from the Red Sea (from Abbildungen und Beschreibungen Conchylien, vol. 3, *Littorina*, pl. 7, fig. 15, about 13 × 11 mm.).

Figs. 2,3. Lectotype of *Littorina radiata* Eyndoux and Souleyet, from Touranne, Viet Nam (BM(NH) 54.7.24.389; 11.5 × 7.6 mm.).

Figs. 4,5. Lectotype of *Littorina novaezelandiae* Reeve, a smooth specimen from Trincomali, Ceylon (BM(NH) 1966124; 13.2 × 9 mm.).

Figs. 6,7. Holotype of *Littorina melanacme* E. A. Smith, from San Cristobal, Solomon Ids. (BM(NH) 76.1.10.67; 9.6 × 6.1 mm.).

Figs. 8,9. Holotype of *Littorina insularis* E. A. Smith [is also holotype of *L. granicostata* Smith] from Christmas Id; Indian Ocean (BM(NH) 1968358, 10.4 × 7.2 mm.).

Fig. 10. Holotype of *Littorina urieli* Biggs, from Eilat, Israel (BM(NH) 1966121, 7.3 × 4.5 mm.).

Figs. 11,12. Lectotype of *Littorina granicostata* Reeve, from Brisbane Water, Australia (BM(NH) 1968318, 6.3 × 4.4 mm.). *L. e. L.*

Figs. 13,14. Holotype of *Littorina eudeli* Sowerby, from Pondicherry, India (BM(NH) 1919, 12.31.33, 12 × 7.4 mm.).

1953 [*Littorina-capsula hagruma* Tokioka and Habe, Publications of the Seto Marine Biological Laboratory, vol. 3, no. 1, pp. 55, 56 (Tanabe Bay, Japan); Habe, 1956, Venus, vol. 19, no. 2, pp. 117-121, fig. B; non-binomial].

1966 *Granulilittorina philippiana* Habe and Kosuge, Venus, vol. 24, no. 4, pp. 313, 328, [figured in] Habe and Kosuge, 1966, Shells of the World in Colour, Hoikusha, vol. 2, p. 20, pl. 6, fig 13 (Goza, Shima Peninsula, Honshu, Japan); Holotype in National Science Museum, Tokyo, 6.8 × 5.2 mm.

1966 *Littorina urieli* Biggs, Journal of Conchology, vol. 26, p. 137, pl. 7, figs 1, 2 (Eilat, Gulf of Eilat, northern end Gulf of Aqaba, Israel) Holotype, BM(NH) 1966121, 7.4 × 5.0 mm.

Types—The types of species described by Philippi in Abbildungen und Beschreibungen Conchylien should be in the Berlin Museum, although I have not been able to confirm their presence. Until this is possible Philippi's figures

must be considered accurate representations of the species, and are here held to be the lectotypes.

It is interesting to note that the lectotype (figured specimen) of *L. radiata* Eydoux and Souleyet is in the British Museum (N.H.), while only two paralectotypes were found at the Paris Museum. Although it would be expected that the 'Bonite' collections would be in the Paris Museum exclusively, a large number of the mollusk types of Eydoux and Souleyet were bequeathed by Souleyet to the British Museum (NH) (see Gray, 1855).

A lectotype for *Littorina novaezealandiae* Reeve was designated by Biggs (1966) and the type locality is here corrected from New Zealand to Trincomali, Ceylon. Other types of Reeve, Smith, Sowerby and Biggs are in the British Museum (NH).

The type of *Littorina chaoi* Yen may be in the Museum Heude, Shanghai. The holotype of *Granulittorina philippiana* Habe and Kosuge is in the National Science Museum, Tokyo.

Nomenclature—The problem of selecting a proper name for this species from among possible synonyms is compounded because of its variability, the fact that somewhat similar species occur elsewhere in the oceans, and because some early workers neglected to cite type localities with their species descriptions. The earliest valid name ap-

pears to be *L. millegrana* Philippi, 1848. (see synonymy). The familiar name *L. granularis* Gray, 1839, has as its holotype a worn specimen which was interpreted by Yen (1942) as being *Tectarius muricatus* Linné. I believe it to be actually a worn specimen of *Nodilittorina miliaris* (Quoy and Gaimard) a west African species. There is also a possibility that *L. reticulata* Anton, 1839, may figure in the competition for the oldest name for this species. However, *reticulata* like *granularis* Gray, has no type locality and the only illustration, that given by Philippi and said to be of Anton's type shows a specimen which is impossible to identify with certainty. *Littorina picta marmorata*, usually considered to be a variant of the Hawaiian species *picta* Philippi, but actually described from the Philippines, and *L. ventricosa* Philippi, are both junior homonyms and therefore fail to qualify as valid names, leaving *millegrana* as the next available taxon.

Records—RED SEA: Eilat, Israel (G. Frankel Coll.). GULF OF ADEN: Aden (ZMC). MADAGASCAR: S.W. Shore Ile des Nattes, S. of Ile Ste. Marie; Ste. Luce, S.E. Madagascar (both USNM). INDIAN OCEAN ISLANDS: E. of Souillac (Savanne R.), Mauritius; Caves Point, W. Mauritius; Reunion; Dunitu Id., N. Male Id., Maldives; Fadifolu Atoll, (all USNM). INDIA: Bandra, N. of Bombay; Bombay; Goa; Cape Comorin (all USNM); Pondicherry (USNM, AMS). CEYLON: S. Shore Fort Frederick, Trincomalee; Pt. de Galle (both USNM). THAILAND: Laem Phan-Pha, Koh Phuket; Koh Huayon, Similan Ids.; Koh Phi Phi (all USNM); Songkla (MCZ); Koh Maiprao; Koh Maiprao (both USNM); Prachuab Khan (MCZ); Koh Nom Sao; Chantaburi Province (MCZ); Koh Sichang; Koh Chala; Rayong; Koh Kut (all USNM). MALAYSIA: Penang (MCZ); Batu Ferringgi, Penang (MCZ); Pulau Ular, Langkawi; Pulau Jerak, W. of Sembilan Ids.; Pulau Anyut, Malacca Str.; Pulau Besar, Malacca Str. (all USNM); Raffles Light, Singapore (USNM, ANSP); Sekudu Id., Johore Str. (USNM); CHINA: Hong Kong; Big Wave Bay, Hong Kong. VIETNAM: (USNM). RYUKYU: Odomari, Okinawa, (USNM). JAPAN: Tsutsu, Tsushima Id., Nagasaki Pref., Kyushu (USNM); Miura Peninsula and Goza, Shima Peninsula, Honshu (both Habe and Kosuge, 1966). PHILIPPINES: Santo Domingo, Batan; Jamelo Bay, S. Shore, Fort Mills, Cavite; Maricaban Id. (all USNM); Corregidor Id. (USNM, ANSP); Mariveles; Grand Is., Subic Bay; Bolinao Bay; Lingayen, all Luzon (all USNM); Marinduque; Pt. Naso, Panay; Zamboanga, Mindanao; Balabac; Bucas Id.; Jolo; Tumindao (all USNM). INDONESIA: Keledjitan, Bantam, Java; Pelabuhan Ratu, Preager, Java; Krakatoa (ZMC); Sulok Id., Jesselton, N. Borneo; Morotai, Halmahera Group, East Indies, Moluccas (all USNM); COCOS (KEELING) ATOLLS: (ANSP). AUSTRALIA: QUEENSLAND: Lizard Id. (AMS); Los Isles (USNM); Halfmoon Bay, nr. Cairns; Fitzroy Id.; Palm Id. (all AMS); Bay Rock (USNM); Royal Seaforth, nr. Lindeman Id.; Brampton Id.; Heron Id., Capricorn Grp. (all AMS); Keppel Bay (USNM); North Keppel Id.; Barney Pt., Port Curtis; Lady Elliot Id.; Bundaberg; Point Vernon, Hervey Bay; Caloundra (all AMS); Cape Cleveland (USNM). NEW SOUTH WALES: nr. Wollongong. WESTERN AUSTRALIA: btwn. Cape Dupuy and Cape Malouet, Barrow Id.; mouth Bigota Creek, W. side Barrow Id.; Airport Beach, Barrow Id.; Broome (all USNM). MELANESIA: S.E. Entrance Woi Bay, Japen Id., West Irian (ANSP); Karkar Id., North-East New Guinea; Matupi Isl. Rabaul, Bismarks; Makira Hbr., San Cristobal, Solomons; Taden Reef, N. of Heinghene, New Caledonia (all AMS); N. of Touho, New Caledonia; E. of Nani Id. (both USNM); Noumea, New Caledonia (AMS, USNM); Suva; Irvines, nr. Malaqereqere, both Viti Levu, Fiji (both USNM). PALAU IDS.: Melekeok, Babelthup Id. (USNM). MARSHALL IDS.: Eniwetok (USNM).

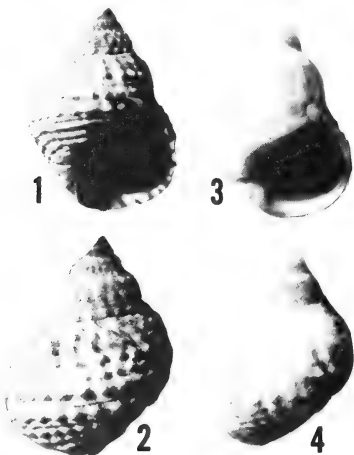


Plate 381. Figs. 1,2. Holotype of *Littorina miliaris* Quoy and Gaimard, 1833, from Ascension Id., Atlantic Ocean (MHNP, 14.6 × 9.4 mm.).

Figs. 3,4. Holotype of *Littorina granularis* Gray, 1839 [eastern Atlantic] (BM(NH) 87.4.26.9, 14.2 × 10 mm.).

Nodilittorina subnodosa (Philippi, 1847)

(Pl. 383, figs. 1-10)

Range—Red Sea and Persian Gulf areas.

Remarks—*Nodilittorina subnodosa* is an exceedingly variable species within its rather narrow area of habitation in the Red Sea and Persian Gulf. The variation is expressed particularly in the degree of shell granulation, different individuals ranging from distinctly nodulose to hardly sculptured. One character apparently rare in *Nodilittorina*, but present in this species, is the white columella, which serves to distinguish *subnodosa* from *natalensis*, its nearest geographic relative. The relationships of *subnodosa* are somewhat obscure. Certain individuals from Persian Gulf populations resemble in part the eastern Atlantic *N. miliaris* Quoy and Gaimard (Rev. H. E. Biggs, personal communication, 1968). I consider that the resemblance is superficial, and that the two are quite distinct. I believe, however, that *subnodosa* may possibly share a common ancestry with *N. miliaris*. The two Persian Gulf populations examined indicate that *N. subnodosa* is more weakly sculptured and may reach a larger size there than in the Red Sea. However, considerable additional comparative material is needed to prove this trend in shell morphology.

Habitat—Shore rocks above high tide line.

Description—Shell reaching 13.8 mm. (about $\frac{1}{2}$ inch) in length, pyramidal to pyramidal-turbinate in shape; average obesity about .66 (38 specimens range from .60 - .70); relatively thick in structure, usually imperforate with some larger and older individuals developing small umbilical opening; sculpture varying from weakly granulose to only moderately nodulose; microscopic sculpture where not worn away consisting of fine closely spaced, wavy spiral threads; axial sculpture consisting of fine, irregular lines of growth. External color, exclusive of nodules and apex, yellowish to pinkish white, occasionally spotted dark brown between nodules; nodules white. Aperture reddish orange to dark brown, with a narrow white band revolving inward from near anterior junction of outer lip and columella; white band obscure in some specimens. Dark apertural coloration usually ending at anterior junction of outer lip and columella; columella white. Apex light to medium brown. Base moderately to considerably flattened, sculptured with spiral, granulose cords. Whorls 5-7, hardly to moderately rounded. Spire usually more than half the length of shell, produced at an angle of from

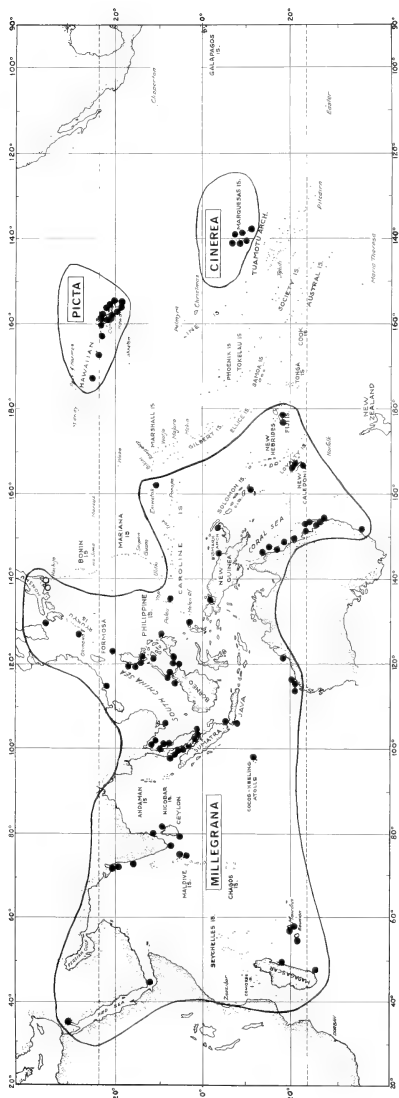


Plate 382. Geographical distribution of *Nodilittorina* (*Granulittorina*) *millegrana* (Philippi), in the Indian Ocean and western Pacific, and of *N. (G.) picta* and *N. (G.) cinerea* (Pease), in Hawaii and the Marquesas Islands respectively.

55-62°. Aperture oval, outer lip moderately thick, tending to be slightly shouldered at the suture; inner lip (columella) thick and moderately flattened; shallowly excavated anteriorly; a flattened, crescent shaped area on base adjacent to columella and an umbilical opening occasionally present in older individuals. Suture indistinct only in more nodulose specimens. Predominant sculpture: three spiral rows of medium sized nodules above periphery on body whorl, often with additional rows of smaller nodules between principal rows; usually 1-3 principal rows of nodules on spire whorls with rows of smaller granulations between. Sculpture in some specimens severely muted, consisting only of spiral rows of granulations showing little or no size separation. Nuclear whorls worn or decollate in all specimens examined, light brown in color; postnuclear whorls spirally nodulose. Operculum thin, chitinous, light brown, paucispiral.

Anatomy grossly similar to *N. natalensis*. Reproduction unknown.

Records—RED SEA: (MCZ); N.E. Museri Id., Dahlak Archipelago, Ethiopia (RNHL); Eilat, Gulf of Aqaba (USNM). PERSIAN GULF: Bushire, Iran (ZMC); near Abu Dhabi, Trucial Coast (USNM).

Types—The location of the type specimens of *Littorina subnodosa* Philippi is not definitely known, although it is probable that they are in the Berlin Museum. Of the two specimens represented in Philippi's illustration, the larger, his fig. 9, is here designated as the lectotype (see pl. 383, fig. 1).

Measurements (mm.)—

length	width	no. whorls	locality
13.8	8.8	5+	Abu Dhabi, Trucial Coast
12.8	8.3	5+	Abu Dhabi, Trucial Coast
12.3	8.6	5+	Abu Dhabi, Trucial Coast
11.9	8.0	6	Abu Dhabi, Trucial Coast
11.1	7.2	5+	Abu Dhabi, Trucial Coast
10.4	7.0	4+	Abu Dhabi, Trucial Coast
9.7	6.8	4+	Abu Dhabi, Trucial Coast
9.0	6.3	4+	Abu Dhabi, Trucial Coast
8.4	5.3	7	Eilat, Gulf of Aqaba
7.2	4.3	6	Eilat, Gulf of Aqaba
6.2	4.2	6	Eilat, Gulf of Aqaba
5.2	3.5	5+	Eilat, Gulf of Aqaba

Synonymy—

1847 *Littorina subnodosa* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 2, p. 161, *Littorina*, pl. 3, figs 8, 9 (Red Sea).

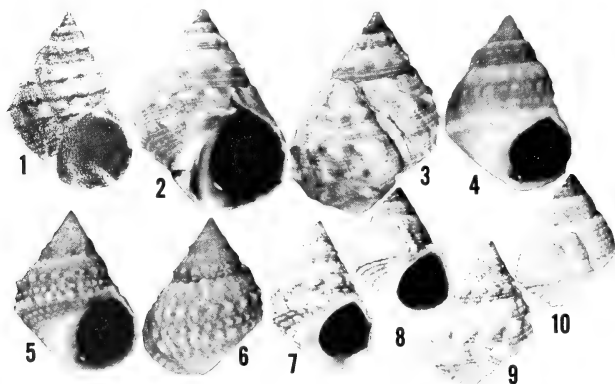


Plate 383. *Nodilittorina (Granulilittorina) subnodosa*. (Philippi, 1847)

Fig. 1. Lectotype figure of *Littorina subnodosa* Philippi, from the Red Sea (from *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina*, pl. 3, fig. 9, about 19 × 12 mm.).

Figs. 2,3. Specimens from an old collection from Gulf of Suez (USNM 23233, 14.5 × 9.6 mm.).

Fig. 4. Rather smooth specimen from near Abu Dhabi, Trucial Oman Coast, Persian Gulf (USNM 669124, 11.8 × 7.8 mm.).

Figs. 5,6. Bushire, Iran, eastern Persian Gulf (USNM 679285, 8.2 × 5.3 mm.).

Figs. 7-10. Strongly nodulose to only moderately granulose specimens from Eilat, Gulf of Aqaba, Red Sea (USNM 671239, 7,9: 8.3 × 5.2 mm.; 8,10: 7.5 × 4.9 mm.).

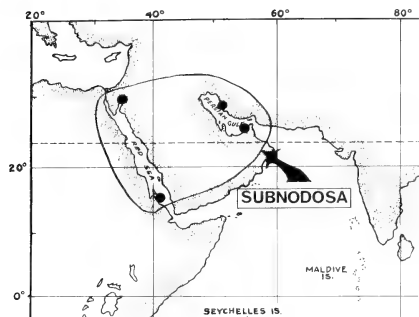


Plate 383a. Geographical distribution of *Nodilittorina* (*Granulilittorina*) *subnodosa* (Philippi) in the Red Sea and Persian Gulf.

Nodilittorina leucosticta

subspecies leucosticta (Philippi, 1847)

(Pl. 384, figs. 1-5)

Range—India and Ceylon.

Remarks—It is extremely difficult to quantify the differences between *G. leucosticta* and *G. millegrana* and on occasion it has seemed impossible to maintain them as separate species. Nevertheless populations of *leucosticta* occur together with *millegrana* in which the individuals belonging to each species are clearly separable. Outside the supposed range of *leucosticta*, no

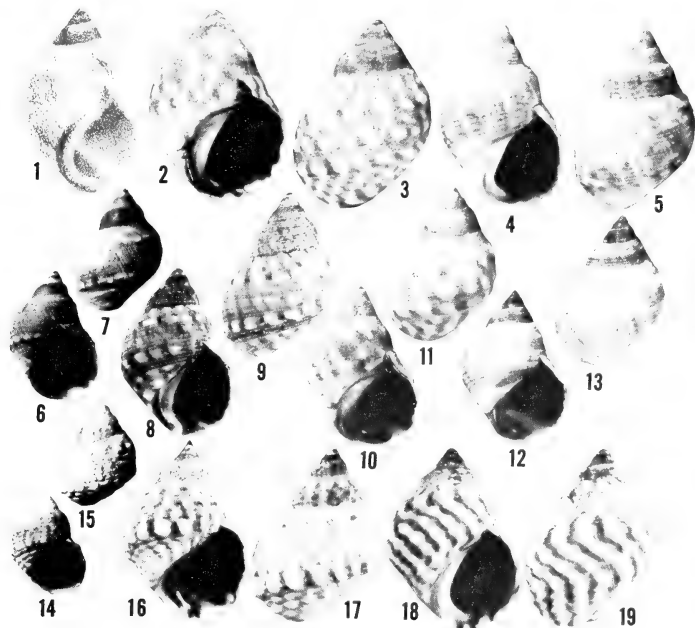


Plate 384. *Nodilittorina* (*Granulilittorina*) *leucosticta* and subspecies.

Figs. 1-5. *N. leucosticta leucosticta* (Philippi).

Fig. 1. Lectotype figure of *Littorina leucosticta* Philippi [Bombay, India] (from *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Littorina* pl. 3, fig. 11, about 8 × 6 mm.).

Figs. 2,3. Pointe de Galle, southwestern Ceylon (USNM 672389, 9.5 × 6.2 mm.).

Figs. 4,5. Goa, India (USNM 442970, 13.1 × 7.8 mm.).

Figs. 6-13. *N. leucosticta biangulata* (von Martens).

—Figs. 6,7. Holotype of *Littorina biangulata* von Martens, from Benkulen [southwest] Sumatra (ZMA, 11 × 7.1 mm.).

Figs. 8,9. Pulau Nias, Mentawai Islands, southwest of Sumatra (USNM 654444, 6.6 × 4.1 mm.).

Figs. 10,11. Mouth Hienghene River, Hienghene Area, New Caledonia (USNM 637368, 10 × 6.3 mm.).

Figs. 12,13. West tip Corregidor Id, Luzon, Philippines (USNM 637360, 9 × 5.5 mm.).

Figs. 14-19. *N. leucosticta feejeensis* (Reeve).

Figs. 14,15. Lectotype of *Littorina feejeensis* Reeve, (BM(NH) 1968319, 7.1 × 5 mm.).

Figs. 16,17. Ovatoa, northwestern Vanua Levu, Fiji (USNM 694772, 7.1 × 4.7 mm.).

Figs. 18,19. Tutuila, Samoa (USNM 488720, 7.2 × 4.7 mm.).

such mixing of phenotypes occurs. It is, therefore, fairly apparent that *G. leucosticta* is a valid species with more restricted range than *mill-egrana* and that the two are clearly separable on shell morphology alone.

The shell of *leucosticta* averages more slender than *milligrana* (obesity .65 vs. .67). The single most striking feature in *leucosticta* is the shouldered appearance of the body whorl in mature individuals. The pattern of hardly raised white nodules on the spiral cords is also distinctive as these are usually interrupted with brown spots; in some populations the shell ground color is dark gray to brown, and here the white semi-nodulated markings are very prominent. The markings are always less pronounced, however, than in *N. pyramidalis*. The aperture in *leucosticta* usually is proportionately more than half the length of shell except in large and apparently anomalous individuals which are not rare in collections.

The subspecies *leucosticta biangulata* von Martens and *l. feejeensis* Reeve replace *leucosticta* s.s. in the East Indies and western Melanesia and in the Pacific Islands respectively. Differences between the subspecies are of a considerably qualitative nature and involve a shift in emphasis of intensity of expressed sculpture and coloration. If these taxa are to be considered subspecies rather than distinct species or even portions of a variational continuum, one must refer to specimens from the several geographical areas cited and to the descriptions of the various morphological peculiarities of each. In such cases species and subspecies concepts are considerably strained.

Habitat—Intertidal on rocks.

Description—Shell reaching 16.2 mm. (about $\frac{5}{8}$ inch) in length, turbinate to elongate oval in shape; average obesity about .65 (22 specimens range from .59 to .70); only moderately thick in structure; imperforate; surface sculptured with rather low and closely spaced spiral cords 2-4 of which, usually three, on body whorl, are stronger than the rest; cords bearing low white, often elongate nodules separated by brown interspaces; shell shouldered about $\frac{1}{3}$ length of body whorl from suture to first strong cord; details of color and sculpture becoming obscured in larger individuals; overall microscopic sculpture where not worn away or otherwise obscured consisting of fine wavy spiral threads. Axial sculpture limited to irregular, often closely spaced lines of growth. External color variable, ranging from

grayish white base color to a dark gray or brown, usually with the low white nodules offering distinct contrast. Aperture medium to dark brown, with a white band revolving inward near anterior junction of outer lip and columella, with occasional fainter bands posteriorly; columella usually lighter colored than rest of aperture. Base slightly flattened; periphery often marked by position of one of stronger spiral cords. Whorls 5-6; spire whorls only moderately rounded; body whorl rather flatsided at its center and shouldered. Spire usually less than half the length of shell, produced at an angle of from about 62-70°. Aperture elongate oval, outer lip only moderately thick; inner lip strongly produced, rather straight, only occasionally slightly bulging posteriorly, with a flattened crescent shaped area on base adjacent to columella callous. Suture well impressed. Body whorl subtly shouldered; predominant sculptural feature: about three well spaced, low spiral cords on body whorl; cords with low white, sometimes elongate nodules, separated by brown color spots; sculpture characteristics often worn away or not evident in older individuals. When present, nuclear whorls about $1\frac{1}{2}$ -2, light brown, smooth; postnuclear whorls becoming darker brown and spirally sculptured. Operculum paucispiral, brown, oval. Radula littorinoid, central tooth only moderately narrow tricuspid.

Animal darkly pigmented on upper surfaces of tentacles, snout and foot. Verge of the *Nodilittorina* type, with a basal enlargement and partially separated penial gland with an accessory flagellum; main portion of verge relatively long and slender, with an open deeply folded sperm duct along its posterior-medial edge. Nothing is known concerning the reproduction and development of this species, although it is suspected to involve a pelagic capsule as yet undescribed.

Measurements (mm.)—

length	width	no. whorls	locality
16.2	9.8	5+	All Bombay, India
15.1	9.3	5+	
14.7	8.7	4+	
13.5	8.3	4+	
11.0	7.1	3+	
10.7	7.2	4+	
9.8	6.8	4+	
8.7	6.1	3+	
7.9	5.2	4+	
6.6	4.5	3+	

Synonymy—

1847 *Littorina leucosticta* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, *Littorina*, p. 162, pl. 3.

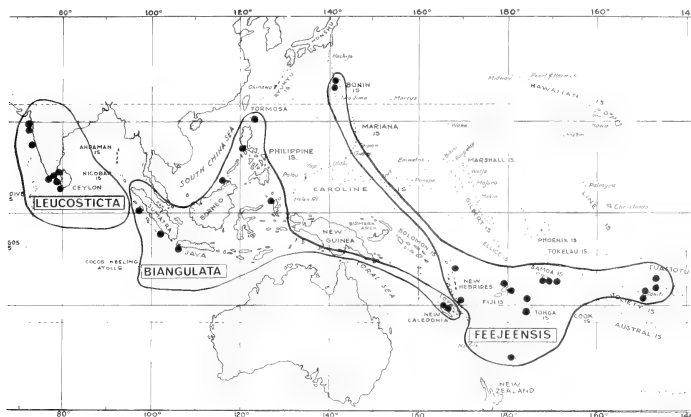


Plate 385. Geographical distribution of *Nodilittorina* (*Granulittorina*) *leucosticta* (Philippi) and of its other two subspecies, *N. (G.) leucosticta biangulata* (von Martens) and *N. (G.) leucosticta feejeensis* (Reeve).

fig 11 [lectotype figure; original measurement about 8×6 mm.] (no locality given; Bombay, India, here designated); lectotype may be in Berlin Museum.

1866 *Melaraphe subgranosa* Dunker, Verhandlungen der Kaiserlich-Königlichen zoologisch-botanischen Gesellschaft in Wien, Jahrgang 1866, vol. 16, p. 913 (Madras [India]); type may be in Berlin Museum; 1867, Frauenfeld, Reise der Österreichischen Fregatte *Norara*, Zoologischen Theil, vol. 2, part 3, *Mollusken*, p. 9, pl. 1, figs. 10 a, b [not fig 10 c which = *G. millegrana* Philippi].

1887 *Littorina leucosticta* 'Philippi' Tryon, Manual of Conchology, vol. 9, p. 299 [error for *L. leucosticta* Philippi, 1847].

Types—Philippi's figure of *leucosticta* (the lectotype figure) depicts a young specimen, a phenotype apparently quite common in India and Ceylon, although this particular oval white spotted form has not been noted in collections from elsewhere. Proportions of the subspecies *G. leucosticta biangulata* are quite different. The lectotype figures of Frauenfeld of *subgranosa* Dunker, show the species in its mature form.

Records—INDIA: Bandra, N. of Bombay; Bombay; Goa; Cape Comorin; Tuticorin; Mandapam Camp. CEYLON: Point de Galle; Columbo (all USNM).

Nodilittorina leucosticta subspecies *biangulata* (von Martens, 1897)

(Pl. 384, figs. 6-13)

Range—East Indies and [?] western Melanesia.

Remarks—*Littorina leucosticta biangulata* von Martens differs from the nominate subspecies in

having typically only two strong spiral sculptural cords on the body whorl. Other sculpture is much suppressed. Shells of this subspecies also tend to be more high spired and therefore the tendency for the spire to be less than half the length of the shell is somewhat reduced. Shells reach 12.4 mm. (about .5 inch) in length; average obesity about .62 (29 specimens range from .56-.65). In the representatives of populations available to me for study, the conservatism in spiral sculpture exhibited by the type is shown in only a few specimens—most develop 3 moderately strong spiral cords bearing subdued white nodules, more like *leucosticta* s.s., but with the above-mentioned narrower profile (see illustrations, also remarks under *leucosticta leucosticta*).

Habitat—On intertidal rocks.

Measurements (mm.)—

length	width	no. whorls	locality
12.4	7.0	6	Touho, New Caledonia
11.0	7.1	6	Holotype: Benkulen Sumatra
10.4	6.8	5+	Jesselton, No. Borneo.
10.1	6.0	5+	Touho, New Caledonia
9.7	6.0	4+	Touho, New Caledonia
8.6	5.2	5+	Touho, New Caledonia
7.8	5.0	6	Jesselton, No. Borneo
7.1	4.4	6	Corregidor Id., Luzon, Philippines
6.7	4.2	5+	Pulau Nias, Sumatra
5.7	3.6	6	Pulau Nias, Sumatra

Synonymy—

1897 *Littorina biangulata* von Martens, in Max Weber, Zoologische Ergebnisse einer Reise in Niederländisch

Ost-Indien, vol. 4, part 1, p. 209, pl. 9, fig 26 (Benkulen [Bengkulu, SW Sumatra]); holotype in Zoologisch Museum Amsterdam, 11 × 7.1 mm.

Records—PHILIPPINES: West tip Corregidor Id. Luzon (ANSP, USNM); Santo Domingo, Batan Id., Batanes Group (USNM). EAST INDIES: Jesselton, N. Borneo; Pulau Nias, (both USNM); Bengkulu, both S.W. Sumatra (Von Martens, 1897, ZMA); Kahatola Id., S. Loloda Ids. Halmahera, Moluccas; Pelabuhan Ratu, Preager, Java (both USNM); NEW CALEDONIA: mouth Hienghene R., Hienghene area; 18 km. N. of Toutho, N.W. New Caledonia (both USNM).

***Nodilittorina leucosticta subspecies feejeensis* (Reeve, 1857)**

(Pl. 384, figs. 14-19)

Range—Pacific Islands, exclusive of Western Melanesia and Hawaii.

Remarks—According to available records *Granulittorina leucosticta feejeensis* replaces *leucosticta* s.s. and *l. biangulata* in the Pacific Islands. It usually has a smaller, more compact shell and spiral sculpture and axial color striping are often strongly expressed, although from the present appearance of Reeve's type, this would not be expected. The type of *L. feejeensis* Reeve has apparently undergone some corrosion of sculpture in over 100 years in the BM(NH) collection. Shells reach 12.7 mm. (about .5 inch) in length; average obesity about .64 (23 specimens range from .61-.72). Most strikingly colorful populations appear to occur in Samoa and Tonga where zigzag dark axial markings stand out against the lighter ground color of the shell (see pl. 384, figs. 18, 19). The general shape of the shell and character of sculpture and coloration clearly relate this species most closely to *leucosticta* and *l. biangulata*.

Habitat—Shore rocks.

Measurements (mm.)—

length	width	no. whorls	locality
12.7	7.8	5+	Ofu, Manu'a, Samoa
11.0	7.5	5	Ofu, Manu'a, Samoa
10.3	6.4	5	Tongatapu
9.4	6.0	5	Lifu, Loyalties
8.7	5.4	6	Arue, Tahiti
8.2	5.7	5	Niuafoou
7.6	5.5	4	Makatea, Tuamotus
7.6	5.1	5	Kermadecs
6.5	4.5	5	Niuafoou
5.6	4.0	4	Tutuila, Samoa

Synonymy—

- 1857 *Littorina feejeensis* Reeve, Conchologia Iconica, vol. 10, *Littorina*, pl. 15, figs 82 a, b. (Feejee [sic] ids.); lectotype BM(NH) 1968319: 7.1 × 5 mm.
 1871 *Littorina vitiensis* Reeve von Martens, Donum Bismarckianum, p. 40; emendation of *L. feejeensis* Reeve, 1857.
 1871 *Littorina* (*Melaraophe*) *vitiensis* Dunker, Malakozoologische Blätter, vol. 18, p. 150 (Hab. ad insulas Vitenses).

1885 *Littorina plena* var. *vitiensis* 'Dunker' Nevill, Hand-List of Mollusca in the Indian Museum, Calcutta, Part 2, p. 139 (Tahiti); emendation of *L. vitiensis* Dunker, 1871.

1885 *Littorina miliaris* var. *fijiensis* 'Reeve' Nevill, *ibid.*, p. 154 (Tahiti); emendation of *L. feejeensis* Reeve, 1857.

1951 *Nodilittorina miliaris* 'Quoy and Gaimard' Habe, Illustrated Catalogue of Japanese Shells, vol. 1, no. 14, p. 92, pl. 14, fig 5; not *N. miliaris* (Quoy and Gaimard) which is Eastern Atlantic species and not from Ascension Id., Pacific = Ponape, Caroline Ids.

Records—(All USNM except where noted). BONIN ISLANDS: Port Lloyd, Chichi Jima; Ani Jima. MELANESIA: Vanikoro, Santa Cruz Group (AMS); Lifu, Loyalties. FIJI: W. side Koro Levu Id. Tavuni. KERMADECS: Raoul, (AMS). SAMOA: Pago Pago, Tutuila; Tafuna, Tutuila; Ofu, Manu'a Group. TONGA: Niuafoou, Niutoua, fringing reef, Tongatapu; Lualea reef, nr. Fatuma, Tongatapu. SOCIETIES: Papeete, nr. Mt. Taharua, Arue, Tahiti; Mt. Taharua, Dist. of Mahina, Tahiti; N. coast of Tahiti. TUAMOTUS: Makatea (USNM, ANSP); N. of Tamao Hbr., Makatea; Maia Id., Tikahau.

***Nodilittorina exigua* (Dunker, 1860)**

(Pl. 386, figs. 1-6)

Range—Coasts of China and Southern Japan.

Remarks—Although *G. exigua* is apparently closely related to *G. millegrana* Philippi, an examination of representatives of Japanese and China coast populations reveals a species that is generally more strongly sculptured, lacks the color striping, has a stronger siphonal trough and more deeply excavated columella than *millegrana*. Habe (1951) synonymized *exigua* under *Nodilittorina granularis* (Gray) but it has been demonstrated that *granularis* is a synonym of the Atlantic species, *N. miliaris* (Quoy and Gaimard). (see remarks under *millegrana*).

Habitat—Shore rocks.

Description—Shell reaching 12.5 mm. (about 0.5 inch) in length, high-spined globose to turbinate; average obesity about .68 (22 specimens range from .64 to .72); moderately thick in structure, imperforate; spiral sculpture usually prominent and consisting of closely spaced raised spiral cords which are alternately granulate and smooth; granulate cords considerably more conspicuous; axial sculpture limited to occasionally coarse oblique lines of growth. External color fairly constant, usually a rather dirty yellowish to grayish white. Aperture medium to dark reddish brown; inner edge of outer lip often lighter colored with spots of brown marking sculptural furrows; with a broad white band revolving inward from near anterior junction of outer lip and columella; columella usually lighter than aperture, occasionally as dark. Base only moderately

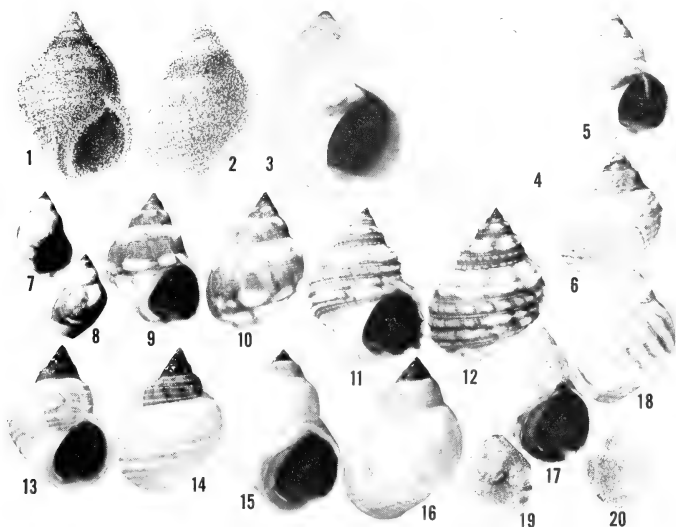


Plate 386. Figs. 1-6. *Nodilittorina (Granulilittorina) exigua* (Dunker)

Figs. 9,10. Smooth form of *N. picta*; Mokuoloe Id., Oahu, Hawaii (USNM 346407, 7.2 × 4.7 mm.).

Figs. 11,12. Nodulose form of *N. picta*; same locality as smooth form (USNM 346411, 8.5 × 5.6 mm.).

Figs. 13-18. *Nodilittorina (Granulilittorina) cinerea* (Pease). Figs. 13,14. Lectotype of *Littorina cinerea* Pease [Marquesas Islands] (ANSP 18811, 7.9 × 5.1 mm.).

Figs. 15,16. Moderately sculptured form, Atuona Bay, Hivaoa Id., Marquesas (ANSP 155486, 8.9 × 5.7 mm.).

Figs. 17,18. Fatu Hiva, Marquesas (USNM 697101, 6.9 × 4.6 mm.).

Figs. 19,20. Holotype of *Littorina iwakiana* Nomura and Hatai, from Tanagura Miocene, Japan (Saitō Hi-on Kai Museum, Sendai, Japan, Reg. no. 6895, 3.8 × 3.2 mm.).

Figs. 1,2. Lectotype figures of *Littorina exigua* Dunker, from Japan (from Dunker, 1861, Mollusca Japonica, pl. 2, fig. 3).

Figs. 3,4. Matsu Shima, Sea of Japan (USNM 601593, 9.8 × 6.8 mm.).

Figs. 5,6. Imaizumi, Kagoshima Bay, Japan (USNM 363708, 8.9 × 6 mm.).

Figs. 7-12. *Nodilittorina (Granulilittorina) picta* (Philippi).

Figs. 7,8. Lectotype of *Littorina picta* Philippi (BM(NH) 1968324, 9.8 × 6 mm.).

flattened; periphery not carinate. Whorls 4-5, rounded. Spire less than half the length of shell, produced at an angle of from 68-78°. Aperture oval; outer lip moderately thick, usually wrinkled at edge; inner lip (columella) moderately well developed, rather deeply excavated anteriorly, with a small denticular bump usually evident one third the distance antero-posteriorly; having a short but pronounced anterior siphonal trough; with a flattened crescent-shaped area on base adjacent to columella callous. Suture moderately well impressed. Nuclear whorls light brown but worn in all specimens examined. Operculum paucispiral, dark brown and oval.

Details of animal and reproduction unknown.

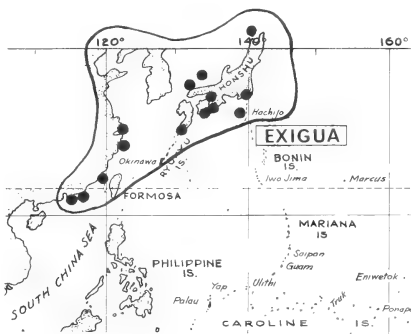


Plate 387. Geographical distribution of *Nodilittorina (Granulilittorina) exigua* (Dunker).

Measurements (mm.)—

<i>length</i>	<i>width</i>	<i>no. whorls</i>	<i>locality</i>
12.4	8.5	4+	Matsushima, Japan
11.2	7.6	4	Matsushima, Japan
10.8	7.3	4+	Komoi, Awaji, Japan
10.2	7.1	4	Matsushima, Japan
9.8	6.3	4	Peiyushan Id., China
9.1	6.2	4	Komoi, Awaji, Japan
8.8	6.3	4	Imaizumi, Japan
8.4	5.9	4	Shirahama, Japan
7.5	5.2	4	Hakodate, Japan
6.9	4.7	3+	Takami, Japan

Synonymy—

- *Littorina granularis* 'Gray' of Authors, *non* Gray, 1839; Gray's holotype, BM(NH) 87.4.26.9 is the Eastern Atlantic species, *Nodilittorina miliaris* (Quoy and Gaimard).
- 1860 *Littorina exigua* Dunker, Malakozoologische Blätter (1859), vol. 6, p. 226 (Japan); 1861, Dunker, Mollusca Japonica, p. 13, pl. 2, fig. 3 [lectotype figure].

Types—The type specimen of *L. exigua* Dunker is probably in the Berlin Museum although it has been impossible to locate it with certainty during the present study. The specimen figured by Dunker in the year following the original description is here considered the lectotype (see pl. 386, figs. 1, 2).

Records—(All from USNM except where noted). CHINA: Sidesaddle Island (Lu-hua shan), Chekiang Province; Peiyushan Id.; Spider Island, Fukien Province; Big Wave Bay, Hong Kong; Cape D'Aguilar, Hong Kong. JAPAN: Hakodate, Hokkaido; Saigo, Dogo Ids. Oki Group; Matsu-Shima; Shirahama, Wakayama Province, Honshu; Toshima, Tanabe Bay, Honshu; Awaji-shima; Kii, Honshu (AMS); Tokyo Bay (ANSP); Imaizumi, Kagoshima Bay, Kyushu (USNM, ANSP); Tosa Shikoku; Hachijo Island, 275 miles S. of Tokyo (both ANSP).

Nodilittorina picta (Philippi, 1846)

(Pl. 386, figs. 7-12)

Range—Hawaiian Islands.

Remarks—The "Painted Littorine" *Granulilittorina picta* is closely related to *G. millegrana*, *G. exigua*, and apparently also to *G. cinerea* Pease. The four species all possess similar variation in sculpture. The relationship with *millegrana* and *exigua* was pointed out by Struhsaker (1968a) who suggested that *picta* is the only one which develops a smooth shell as well as a granulose one [some populations of *millegrana* develop smooth shells also; see pl. 386, fig. 7, 8, 9, 10]. The possible selective processes causing the extensive shell variation in *picta* are well discussed by Struhsaker (*ibid.*). It is probable that morphology of most wild populations is under the positive control of natural selection there being few if any mutations which survive for very long in nature without some selective value. [The survival of so many natural populations is coming under the aegis of man, that the beneficial "weeding out" effect of unsuitable elements by natural selection may be considerably lessened. One wonders what eventual effect this will have on all species involved, including *Homo sapiens*.] It is, therefore, most likely, as pointed out by Struhsaker that each of the shell forms of *picta*, from highly granulose to smooth, has survival value under particular ecological conditions, i.e. smoother forms survive best in wave-swept areas, and sculptured forms occur in sheltered localities. The morphological differences are apparently genetically linked, but survival of the resultant phenotype is under the control of environmental selection.

The subspecies name *L. picta marmorata* Philippi has generally been used for one of the variations of *picta* in Hawaii. The name *marmorata* was not validly introduced by Philippi in connection with the original description of *picta* (see synonymy) but was mentioned and figured in the "Abbildungen" the following year with the added locality "provincia Ilocos borealis insulae Lucon" [Philippines]. Both figure and locality indicate that *L. picta marmorata* is a synonym of *G. millegrana*. It is likely that Philippi, himself, did not clearly discriminate between the populations of *picta* from Hawaii and some of the forms of *millegrana* occurring in the Philippines. They are indeed similar and this has given rise to considerable confusion, wherein extra Hawaiian *Granulilittorina* are called "*picta*." As the mem-

bers of this subgenus all appear to be fairly closely related it is perhaps a matter of personal preference whether one considers them separate species or geographic subspecies. In the case of *picta* and its allies it is here considered less confusing to consider them separate species.

In likening *picta* to *neritoides*, Philippi indicated that he was describing a rather smooth little shell, and the three syntypes of *picta* in the British Museum (NH) reinforce this view. In my experience, the name "*marmorata*" has been used for the more highly sculptured forms, although certainly the figure given by Philippi does not show such a shell. It would appear that the local interpretations of these names have come about with usage. However, when the situation is examined closely it is found that *picta* is the only valid name for this species; *marmorata*, as shown above, not only is a synonym of another species but is preoccupied by *L. marmorata* Pfeiffer, 1839 [= *L. saxatilis* Oliv.]. Tinker's (1952) suggestion that *picta* is considered by some to be a synonym of *L. planaxis* (eastern Pacific) is understandable. Certain populations especially of young *planaxis* show similarities to *picta* in color variation. They are, however, in distinct generic groups, as well as being separate species (see List of Taxa). The connection between *L. planaxis* and *picta* probably dates from Tryon's (1887) synonymy.

Habitat—Shore rocks above high tide line (see Struhsaker, 1968a).

Description—Shell reaching 12.9 mm. (about 0.5 inch) in length; rather conic to turbinate in shape; average obesity about .64 (20 specimens range from .59-.69); moderately thick in structure, imperforate; surface often smooth, or only microscopically spirally striate; but often bearing raised, rather strong and granulose spiral cords on spire and body whorls [granular sculpture most similar to that in *G. millegrana*, but whorls shouldered as in *G. leucosticta* and its subspecies]. Axial sculpture consists of faint to rather coarse, irregular lines of growth. External color very variable; generally consisting of grayish to yellowish white ground color "painted" with dark-brown markings, a common pattern on body whorl being the center of whorl dark, with area above and below divided into light colored sections by wavy brown lines; The latter not at all constant and brown painting may be minimized or maximized; more highly sculptured shells appear darker overall. Aperture medium to dark brown and may be brown and white mottled as is

exterior; with an often diffuse or interrupted white band revolving inward from near anterior junction of outer lip and columella; columella usually light tan; inner edge of outer lip white or with a few white spots. Base slightly flattened; periphery occasionally with a weak to moderate keel. Whorls 5-6, not very well-rounded, body whorl distinctly flat-sided. Relative lengths of spire and aperture about co-equal, one sometimes exceeding the other apparently indiscriminately; spire produced at an angle of from about 60-65°. Aperture oval; outer lip moderately thick; inner lip (columella) only moderately developed, with a flattened crescent shaped area on base adjacent to columella callus. Suture well impressed. Sculpture varying from virtually smooth to markedly spirally striate with coarse granulations. Nuclear whorls light brown anteriorly, darker brown posteriorly on each whorl, smooth and unsculptured; in shells which will be granulosely sculptured, this begins after about 2½ nuclear whorls; in shells which never develop coarse sculpture, only low spiral striae begin after nuclear whorls. Operculum paucispiral, brown, oval. Radula littorinid, 2-1-1-1-2, central tooth rather narrow.

Details of animal are from Whipple (1965): In males base of penis is red as is testicular duct; there is an enlargement at base of penis partially separated from a penial gland containing an accessory flagellum; sperm groove runs along posterior edge, deeply folded. Reproduction oviparous, producing a sculptured pelagic capsule about 180µ in diameter, with single egg about 75µ in diameter. According to Struhsaker (1968b) a swimming veliger hatches in about 3 days and the larva settles and metamorphoses about 21 days after spawning.

Measurements (mm.).—

length	width	no. whorls	locality
12.9	8.0	5+	Hawaiian Ids.
12.7	8.0	6	Waikiki, Oahu
11.8	7.9	5	Waikiki, Oahu
11.1	6.6	5	btwn Waipio and Pearl City, Oahu

10.9	6.8	5	Diamond Head, Oahu
10.0	6.8	5	Launiupoko, Maui
9.9	6.1	5	btwn Waipio and Pearl City, Oahu
9.6	6.1	5	Paia Beach, Maui
9.1	5.9	6	Wainini, Kauai

Synonymy—

- 1846 *Littorina picta* Philippi, Proceedings of the Zoological Society of London, for 1845, part 13, p. 139 (Hawaii); lectotype in BM(NH) 1968324: 9.8 × 6.0 mm.; 1847, as *Littorina picta* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, *Littorina* p. 166 [not *L. picta marmorata*, *ibid.*, p. 167, pl. 3, fig. 26 (from Luzon, Philippines) = *G. millegrana* Philippi].
- 1857 *Littorina picta* Philippi, in Reeve, Conchologia Iconica, vol. 10, *Littorina* pl. 15, figs 80 a, b, 81.
- 1887 *Littorina planaxis* 'Nuttall' Tryon, Manual of Conchology vol. 9, p. 248, pl. 44, fig 57 [only in part; includes *L. picta* Philippi as synonym; not *L. planaxis* 'Nuttall' Philippi, 1847, an eastern Pacific species.

Types—Three syntypes of *Littorina picta* Philippi were found in the British Museum (NH) 1968324. Of these, the one most nearly approximating the original measurements is here designated lectotype. Original measurements given by Philippi were: "Alt. 4, diam. 3 lin." which yields the following millimeter measurements based on a "German Line" equaling 2.18 mm. (Rehder, 1945): length 8.7, width 6.6 mm. The actual measurements of the designated lectotype are 9.8 × 6.0 mm., fairly close to the original, and here considered within the limits of a possible measurement error. (see pl. 386, figs. 7, 8)

Records—HAWAIIAN ISLANDS: Laysan Island : La Perouse Rock, French Frigate Shoals; Nihoa Island (all BPBM). KAUAI ISLAND: Nawiliwili (BPBM); Koloa (ANSP); Haena (BPBM). OAHU: Kahuku Point (BPBM); Laie (ANSP, MCZ); Kahana; Mokolii Island, Kaneohe Bay; Mokuoloe Island; Moku Manu; Kailua; Manana (Rabbit Island) (all BPBM); Diamond Head; Waikiki (both ANSP, MCZ, BPBM); Pearl Harbor; Barber's Point (both BPBM); off Puu Maililili (MCZ); E. of Waianae (ANSP); Makua (MCZ); Haleiwa (ANSP); Waimea (BPBM). MOLOKAI: Pauwahu; Papohaku (both BPBM); Moomomi (BPBM, ANSP); MAUI: Lahaina (ANSP). KAHŌLOAWE ISLAND: (ANSP). HAWAII: Hilo (ANSP, BPBM, MCZ); Kalapana; Waiahukini, Kau; Hoopuloa (all BPBM); Refuge City; Honaunau Bay, Kona (ANSP); Keauhou (BPBM); Kahaolu (ANSP); Kaulana, Kau; Tawai, Kalalaa, at stream outlet (both BPBM).

Nodilittorina cinerea (Pease, 1869)

(Pl. 386, figs. 13-18)

Range—Marquesas Islands.

Remarks—*N. (Granulilittorina) cinerea* is closely related to *N. picta* of Hawaii and shows much of the same sort of variation from smooth to granulose sculpture. A color pattern is also evident in occasional specimens of *cinerea*, but never to the same degree as in *picta*. As in the case of *picta*, *cinerea* is also quite closely related to the other species of the subgenus *Granulilittorina*, and some of its forms are very close to *N. millegrana*. Major distinguishing features are (1) the gray color as indicated by Pease's name "*cinerea*", which never reaches the marbled coloration of *picta*, (2) the whorls which may become relatively broadly shouldered, and (3) the degree of sculpture, ranging from almost smooth to fairly granulose spiral cords. According to available records, this species is endemic in the Marquesas Islands.

Habitat—In splash zone, above high tide line, in cracks in lava, crawling on rock surface at night (personal communication, H. A. Rehder; from observations made at Nuku Hiva, Marquesas Islands, 1967).

Description—Shell reaching 9.0 mm. (about $\frac{1}{3}$ inch) in length; turbinate to shouldered-turbinate in shape; average obesity about .65 (20 specimens range from .58-.71); only moderately thick in structure; imperforate; sculpture of low to rather distinct spiral cords; cords smooth or granulose; whorls varying from only slightly to rather distinctly shouldered; axial sculpture consisting of faint to coarse growth lines and furrows; occasionally specimens have a deep, ragged axial mark of growth interruption. External ground color somewhat variable from grayish white to distinct bluish gray, the latter especially in the young; occasional patterning consists of irregular darker gray to brown zigzag lines and flammules. Aperture medium reddish brown to dark brown with a white band revolving inward from near anterior junction of outer lip and columella; columella usually colored about as aperture or slightly lighter; inner edge of outer lip white. Base somewhat flattened; periphery not keeled, whorls shouldered for about $\frac{1}{3}$ the distance anterior to suture. Whorls about 4-6, not too well rounded but rather tending to be straight-sided. Relative

lengths of spire and aperture about coequal or spire slightly shorter. Spire produced at an angle of from about 60-67°. Aperture widely oval; outer lip moderately thick; inner lip (columella) moderately strong, with an often well depressed crescent shaped area on base adjacent to columella callous; the depression rarely approaching an umbilical chink. Suture well impressed. Sculpture varying from specimens with hardly raised spiral cords to those exhibiting distinct well raised cords with granulations on all whorls. Nuclear whorls light brown anteriorly, dark brown posteriorly smooth and unsculptured; nucleus about 2 whorls in extent; first postnuclear whorl smooth, subsequent whorls with spiral sculpture; overall microscopic spiral sculpture consisting of fine wavy spiral threads. Operculum paucispiral light brown, oval. Radula littorinid, 2-1-1-1-2, central tooth rather narrow.

Animal similar to other *Nodilittorina*. Nothing is known concerning reproduction and larval development; probably similar to *G. picta*.

Measurements (mm.)—

length	width	no. whorls	locality
9.0	5.8	5+	Hiva Oa, Marquesas
8.7	5.3	4+	Hiva Oa, Marquesas
8.5	5.6	5+	Hiva Oa, Marquesas
8.2	4.8	6+	Hiva Oa, Marquesas
8.1	5.2	4+	Hiva Oa, Marquesas
7.9	5.1	6	Lectotype, Marquesas
7.3	5.2	4+	Fatu Hiva, Marquesas
7.0	4.7	3+	Fatu Hiva, Marquesas
6.8	4.6	4+	Fatu Hiva, Marquesas
6.4	4.3	4+	paralectotype, Marquesas

Synonymy—

1869 *Littorina cinerea* Pease, American Journal of Conchology, vol. 5, part 2, p. 78, pl. 8, fig. 14 (Marquesas Islands); lectotype ANSP 18811: 7.9 × 5.1 mm.

Types—There are three syntypes of *Littorina cinerea* Pease in the ANSP. Of these, one, most resembling the figure associated with the original description, is here designated lectotype: ANSP 18811 (pl. 386, figs. 13, 14). Its measurements: length 8.1, width 5.2, are fairly close to the originals given by Pease: 7 × 5.5 mm. The lectotype and two paralectotypes fairly well fulfill Pease's descriptive comments: "... transversely granosely ridged or smooth ... cinereous or whitish, apex blackish ..."

Records—MARQUESAS ISLANDS: Nuku Hiva (ANSP; USNM); Ua Pou, Tahuata (both USNM); Ua Huka (ANSP); Hiva Oa (ANSP; USNM); Fatu Hiva (USNM).

Nodilittorina iwakiana
(Nomura and Hatai, 1936)

(Pl. 386, figs. 19, 20)

Range—Miocene, Japan.

Remarks—The tiny species described by Nomura and Hatai appears to show closest affinity with the members of the subgenus *Granulilit-*

torina. Details of sculpture given by the authors suggest that this fossil may be related to *G. millegrana* Philippi.

Synonymy—

- 1936 *Littorina iwakiana* Nomura and Hatai, Saito Ho-on Kai Museum Research Bulletin, no. 10, p. 144, pl. 16, figs 16a, b. (Tanagura Miocene, Okada, Japan); unique holotype in Saito Ho-on Kai Museum, Sendae, Japan, Reg. No. 6895; 3.8 × 3.2 mm.

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THE FAMILY LITTORINIDAE IN THE INDO-PACIFIC

Part II. The Subfamilies Tectariinae and Echinininae

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Abstract

The classification of tropical Indo-Pacific Tectariinae and Echinininae (Mollusca: Mesogastropoda: Littorinidae) has been revised. Seven Recent and three Tertiary fossil species belonging to three generic or subgeneric groups are redescribed and figured. Complete systematic synonymies are given, together with discussions of relationships, biology and zoogeography. A list is given of world-wide members of Tectariinae and Echinininae.

Introduction

In Part I of Indo-Pacific Littorinidae the species belonging to the subfamily Littorininae were reviewed by Rosewater (1970). The present section covers the subfamilies Tectariinae and Echinininae. As yet not covered are such groups as *Bembicium* and its allies and *Cremnoconchus*, although they both occur in the Indo-Pacific region. They are here considered to constitute at least subfamily groups, if not separate families (see Bibliography in Rosewater, *ibid.*, p. 427; Anderson, D. T., 1960, and also Anderson, H., 1958; also see Prashad, 1925 and Kesteven, 1903). The many Antarctic littorinids were excluded from Part I of this study since actually they are out of the geographic area of the tropical Indo-Pacific (see Powell, 1951 and Dell, 1964).

The Littorininae, Tectariinae and Echinininae differ in habitat preference and in morphology in a number of aspects. Echinininae tend generally to live rather high on the shore. Tectariinae are next and Littorininae usually are nearest to the sea, although considerable variation exists, the genus *Nodilittorina* having some high-living species. The differentiation of the three subfamilies also is based on the following morphological grounds. In Littorininae the radula is of the generalized littorinid type with some narrowing of the central tooth in *Nodilittorina*; opercula are paucispiral; penises are adorned with a few penial glands but otherwise are not particularly complicated.

In the Tectariinae the lateral radula tooth is partitioned and appears thickened and differently oriented than in either Littorininae or Echinininae; the opercula are mesospiral (see below); penises are abundantly supplied with glands and are also papillose on non-glandular surfaces. The shells in both Littorininae and Tectariinae usually are imperforate although the subgenus *Cenchritis* is an exception in the latter subfamily.

In Echinininae the radula is not unusual, the subgenus *Tectininus* excepted, where reduction has taken place; opercula are multispiral; shells are umbilicate, usually; penises are supplied with a number of penial glands near the base. In the possession of an umbilicus *Cenchritis* could be considered to form a bridge between *Tectarius* and *Echininus*. In general, however, *Tectarius* appears to be more closely related to *Littorina* in its conservative characters, while *Echininus* may be considered a specialized group perhaps evolving toward a land environment. These three subfamily groups provide a convenient and apparently natural framework upon which to arrange the contained genera and species (see illus-

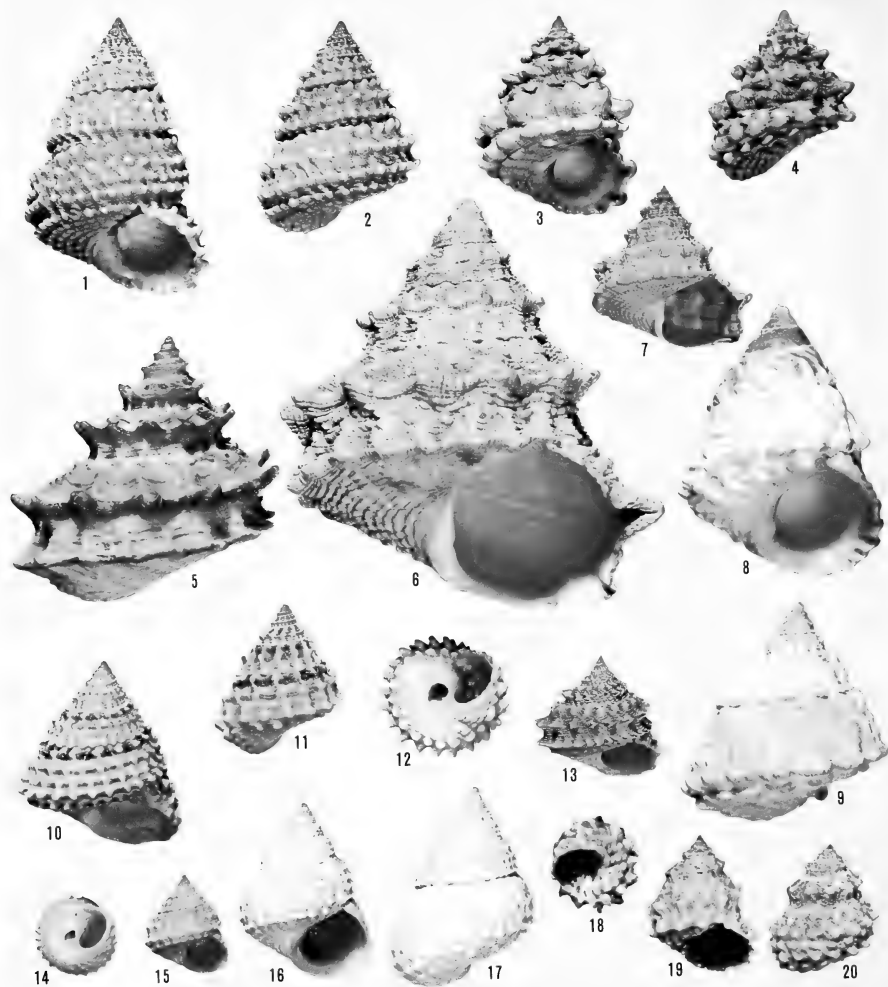


Plate 388. Subfamilies Tectariinae and Echininae
(explanation on opposite page; all figures about natural size)

trations of these morphological differences in Rosewater, 1970, and in this paper).

Most *Tectarius s.s.* and *Echininus s.s.* are living today only in the East Indian area. With the exception of *Tectarius grandinatus* whose range extends eastward to Polynesia, all other species are inhabitants of the raised, weathered coral reef shorelines found in the Western Pacific Arc (personal observations, 1970). It can only be assumed that this niche provides the requirements essential for the existence of these species as they are to be found nowhere else.

The fossil record provides very few clues to the origin of these groups. There are only three Tertiary fossil species described from the Indo-Pacific and these probably belong in three separate generic taxa. The oldest of these, *T. songoense* Martin, from the Upper Eocene of Java, probably represents nearly the earliest appearance of *Tectarius*. As mentioned in Part I, littorinid fossils are exceedingly difficult to separate from Trochidae and Turbinidae, and this is no less true for *Tectarius* and *Echininus*. Probably, however, these groups made their appearance in the early Tertiary within the region where they have developed, and with the exceptions of *Echininus (Tectininus) nodulosus* and *Tectarius (Cenchritis) muricatus*, both of the western Atlantic, they have remained there.

Opercula

The opercula of Indo-Pacific Littorinidae require special comment (see pl. 389). All are made up of conchiolin, and those of members of the subfamily Littorininae, including *Littorina*, its subgenera, and *Nodilittorina* are usually paucispiral and rather oval in shape with the nucleus at the side and nearer one end (oligogyrous spiral type of Fretter, et al., 1962, pp. 79,80). In the Echinininae, the basic plan of the operculum differs from that of other littorines. It is the type

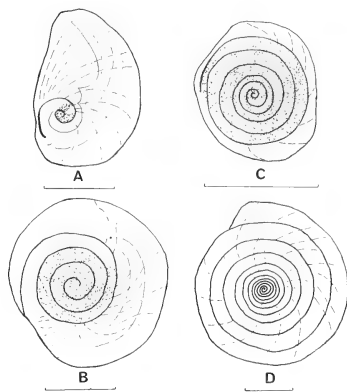


Plate 389. Opercula of Littorinidae and Trochidae.

Fig. A. Paucispiral operculum of *Littorina (Littorinopsis) scabra* (Linne) from Mokuoloe Id., Kaneohe Bay, Oahu (USNM 339388).

Fig. B. Mesospiral operculum of *Tectarius rusticus* (Philippi) from Troughton Chain, northern Western Australia (WAM 1787-69).

Fig. C. Multispiral operculum of *Echininus cumingi* (Philippi) from near Davao City, Mindanao, Philippines (WAM 1566-70).

Fig. D. Multispiral operculum of *Trochus niloticus* Linné, from Makuluva, Viti Levu, Fiji (USNM 531827). Lines under each figure represent 5 mm.; stippled areas are thickened and dark-brown in color; non-stippled areas are light horn color and transparent.

of operculum which is called in other groups, such as Trochidae, a multispiral operculum (polygyrous spiral type of Fretter, et al., *ibid.*) although not so extreme as that figured by Fretter (*ibid.*, p. 80, fig. 43A; also see our pl. 389, fig. D.). The operculum is circular in outline and moderate to small in size. The nucleus is decidedly central in location and growth proceeds outward from the center in multiple, fairly evenly spaced gyrations (pl. 389, fig. D). The operculum in Tectariinae (fig. B) is intermediate in form between

Explanation to plate 388 (opposite page)

Figs. 1,2. *Tectarius grandinatus* (Gmelin) from Palmerston Atoll, Cook Islands (USNM 685165).

Figs. 3,4. *Tectarius tectumpersicum* (Linne). Fig. 3, from Stirling Isle, Treasury Ids., Solomon Islands (USNM 600370); Fig. 4, from "East Indies" (USNM 131450).

Figs. 5-7. *Tectarius pagodus* (Linne). Fig. 5, from "East Indies" (USNM 18966); Fig. 6, from the Philippines (USNM); Fig. 7, a young specimen from Polillo, Philippines (USNM 311141).

Figs. 8,9. *Tectarius rusticus* (Philippi) from Buccaneer Archipelago, Western Australia (USNM 684713).

Figs. 10,11 *Tectarius rugosus* (Wood). Fig. 10, from Pacific (USNM 304587); Fig. 11, from Davao Bay, Mindanao, Philippines (USNM 654034).

Figs. 12,13. *Echininus cumingi cumingi* (Philippi) from Hervey Ids., Cook Ids. (USNM 42452).

Figs. 14,15. *Echininus cumingi spinulosus* (Philippi) from Kadena Circle, Okinawa, Ryukyu Ids. (USNM 664658).

Figs. 16,17. *Tectarius (Cenchritis) muricatus* (Linne), from Boca de Camarioca, Matanzas, Cuba (USNM 599944).

Figs. 18-20. *Echininus (Tectininus) nodulosus* (Pfeiffer). Fig. 18, from Hog Island, Bahamas (USNM 603911); Figs. 19, 20, from Mujeres Harbor, Quintana Roo, Mexico (USNM 662308).

Littorininae and Echinininae, being large and rather rounded in outline, with a slightly acentric nucleus and having a number of gyrations more than the paucispiral type but less in number than the multispiral type. The Tectariinae opercular type is here termed the mesospiral or mesogyrous spiral type. The presence of the three opercular types in Littorinidae may be considered to have evolutionary significance, and possibly is related to selection for a better aperture sealing mechanism in animals which have considerable vertical distribution on the shore line: in order, proceeding from low toward higher shore habitats—Littorininae, Tectariinae, Echinininae.

Reproduction

To my knowledge nothing is known concerning reproduction in either Tectariinae or Echinininae with the exception of *Tectarius (Cenchritis) muricatus* (Linné) which produces a pelagic capsule (see Lebour, 1945, and Lewis, 1960, references in Rosewater, 1970 p. 05–276). Field and laboratory studies are needed to discover details of the life histories of the remaining species. However it is likely that most of these snails also produce eggs encased in pelagic capsules which undergo development in the sea. Abbott (1954) noted that Lebour (*ibid.*) stated that some of the Bermuda littorinids that live above high tide line migrate to the water to spawn. It is suspected that this also is the case with many of the Indo-Pacific species.

Acknowledgments

The persons and institutions acknowledged in Part I of this study (see Rosewater, Indo-Pacific Mollusca, vol. 2, no. 11, p. 425) also are thanked here. In addition, I acknowledge the following for their help in making possible the examination in the field of most of the species of *Tectarius* and *Echininus* during the National Geographic Society—Mariel King Memorial Expedition to the Moluccas Islands, Indonesia, May to July 1970: the late Mariel King, Mrs. Grace King, T. H. Richert, C. Beal, C. M. Burgess, B. R. Wilson, and the National Geographic Society. The Government of Indonesia graciously provided clearance for the vessel *Pele* to work in the Moluccas Islands. Mr. Kasim Moosa and Mr. Sukarno, both of the Institute for Marine Research, Djakarta, accompanied the expedition and provided assistance of many kinds.

List of Recognized Taxa

Below is a list of the Tertiary fossil and Recent species herein recognized as belonging in the subfamilies Tectariinae and Echinininae. The few fossil taxa are preceded by a dagger [†].

Family Littorinidae Gray, 1840

Subfamily Tectariinae, new subfamily

GENUS *Tectarius* Valenciennes, [1832]

Subgenus *Tectarius* Valenciennes, [1832]

rugosus (Wood, 1828). **Type.** Recent, western Pacific

grandinatus (Gmelin, 1791). Recent, Pacific islands

pagodus (Linné, 1758). Recent, western Pacific

tectumpersicum (Linné, 1758). Recent, western Pacific

rusticus (Philippi, 1846). Recent, northern Australia

† *songoense* (K. Martin, 1931). Eocene, Java.

Subgenus

† *Subditotectarius* Ladd, 1966

† *rehderi* Ladd, 1966. **Type.** Miocene, Marshall Islands.

Subgenus *Cenchritis* von Martens, 1900

muricatus (Linne, 1758). **Type.** Recent, tropical western Atlantic.

Subfamily Echinininae, new subfamily

GENUS *Echininus* Clench and Abbott, 1942

Subgenus *Echininus* Clench and Abbott, 1942

cumingi cumingi (Philippi, 1846). **Type.** Recent, western Pacific

cumingi spinulosus (Philippi, 1847). Recent, western Pacific

† *adelaidensis* (Cotton, 1947). Pliocene, South Australia.

Subgenus *Tectininus* Clench and Abbott, 1942

nodulosus (Pfeiffer, 1839). **Type.** Recent, tropical western Atlantic.

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Key to the Tectariinae and Echininae

The following key is to the genera and subgenera of these two subfamilies. It is based upon the shell and externally observable characters. Page numbers are given for Indo-Pacific groups

only, since Western Atlantic taxa are not treated in detail in the present paper. For a key to the Littorininae, see vol. 2, no. 11, p. 430 [p. 05-278].

- 1a Shell umbilicate 2
 1b Shell not umbilicate 3
- 2a Shell spinose, with partially open spines, shell about as wide as high, operculum multispiral (see pl 389) *Echininus* p. 526
 2b Shell not spinose, nodulose, higher than wide, operculum not multispiral . . . *Cenchritis*
- 3a Shell spinose, operculum mesospiral. *Tectarius* p. 513
 3b Shell nodulose, fossil *Subditotectarius* p. 524
 3c Shell moderately spinose, operculum multispiral *Tectinus*

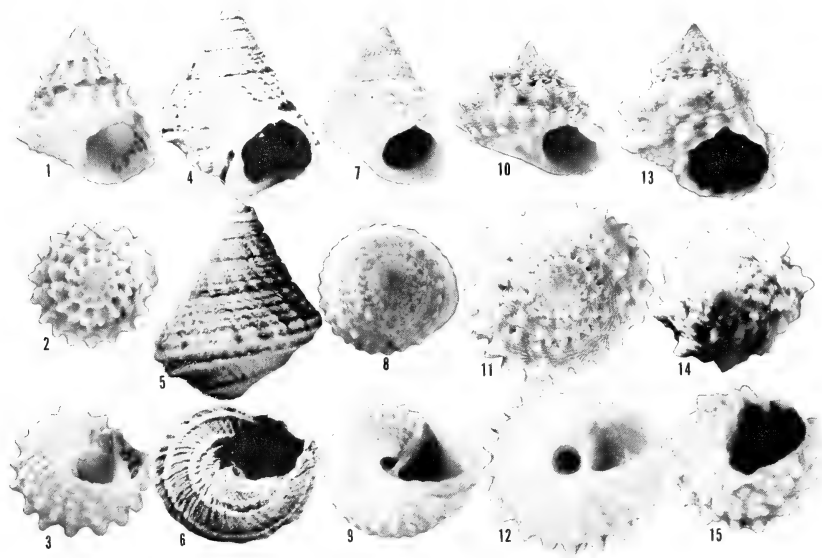


Plate 390. Type-species of Genera and Subgenera of Tectariinae (Figs. 1-9) and Echininae (Figs. 10-15) illustrating sculpture, arrangement of spines, and presence or absence of umbilici.

Figs. 1-3. *Tectarius (Tectarius) rugosus* (Wood); Davao Bay, Mindanao, Philippines (USNM 654034; 23.1 × 17.8 mm.).
 Figs. 4-6. *Tectarius (Subditotectarius) rehderi* Ladd; early

Miocene, Marshall Islands (Holotype, USNM 648342; 2.8 × 2.4 mm.).
 Figs. 7-9. *Tectarius (Cenchritis) muricatus* (Linné); Matanzas, Cuba (USNM 599944; 26.1 × 17.9 mm.).
 Figs. 10-12. *Echininus (Echininus) cumingi* (Philippi); Cook Islands (USNM 42452a; 17.2 × 17.5 mm.).
 Figs. 13-15. *Echininus (Tectinus) nodulosus* (Pfeiffer); Cozumel Id., Mexico (USNM 662806; 14.4 × 12.2 mm.).

Subfamily Tectariinae, new subfamily

Genus *Tectarius* Valenciennes, [1832]

Type: *Tectarius rugosus* (Wood, 1828)

The genus *Tectarius sensu lato* includes the nominate subgenus, *Tectarius*, whose type-species *T. rugosus* Wood (= *T. papillosus* 'Lamarck' of authors) has one of the more conservatively sculptured shells of the group. *Tectarius sensu stricto* is a wholly Indo-Pacific group, having its present population center in the Western Pacific Arc. The monotypic subgenus *Cenchritis* von Martens contains only *T. (C.) muricatus* (Linné), of the tropical western Atlantic (see pl. 388, figs. 16, 17). *Subditotectarius* Ladd, 1966, is monotypic for the fossil *T. (S.) reheri* Ladd, of the Miocene of the Marshall Islands. Only species belonging to *Tectarius* s.s. and *Subditotectarius* will be considered here.

Tectarius appears more closely related to *Littorina* than to *Echininus* because of greater similarities in morphology, general shell characters, the absence of a truly multispiral operculum, a broader, less modified central radula tooth, and the usual lack of an openly umbilicate shell.

Subgenus *Tectarius sensu stricto*

Moderately large, pyramidal to turbanate, non-umbilicate littorinids with from rather strongly spinose to nodulose or papillose shells; generally living at or above high tide line. Radula littorinoid, the central tooth somewhat narrowed, the lateral tooth with an embayment and usually developing a medial vertical ridge or partition. In males the penis is large and well-supplied with glands along most of its lateral edge, the remainder papillose, and with an open but deeply folded seminal duct. Operculum rounded, mesospiral (see **Opercula** in Introduction). Aperture plicate within; with a columellar swelling or tooth.

Synonymy—

- 1798 *Cidaris* Röding, Museum Boltenianum, part 2, p. 84; type-species by subsequent designation, Hermannsen, 1847: *Trochus pagodus* Linné; non *Cidaris* Leske, 1778, nor Swainson, 1840.

- [1832] *Tectarius* Valenciennes, *Coquilles*, in Humboldt and Bonpland. Voyage aux régions équinoxiales du Nouveau Continent. Observations de Zoologie, vol. 2, p. 271; type-species by subsequent designation Clench and Abbott, 1942: *Trochus coronatus* Valenciennes [= *Tectarius rugosus* (Wood)]. ICZN Opinion 871.
- 1839 *Pagodus* Gray, in *Molluscous Animals: The Zoology of Captain Beechey's Voyage*, p. 141; type-species by Monotypy and by absolute tautonymy, *Monodonta pagodus* Lamarck [= *Tectarius pagodus* (Linné)].
- 1840 *Pagodella* Swainson, A Treatise on Malacology, pp. 207, 219, 221 [refers to *Pagodella echinata*, nomen nudum] 351; refers to *P. major* Martini - Chemnitz, pl. 163, figs 1541, 1542 [= *Tectarius pagodus* (Linné)] and to *T. tectumpersicum* ibid., fig. 1543, 1544; type-species here designated: *Tectarius pagodus* (Linné).
- 1840 *Echinella* Swainson, ibid., pp. 207, 221, 352; refers to *E. granulata* Swainson [nomen nudum] and to *E. coronaria*, Tableau Encyclopedique et Methodique, pl. 447, fig 6 [= *Monodonta coronaria* Lamarck = *Tectarius grandinatus* (Gmelin)]; type-species by monotypy, *Tectarius grandinatus* (Gmelin) [also see Clench and Abbott, 1942]; not *Echinella* Bory St. Vincent, 1824.
- 1846 *Fectaria* Philippi, Abbildungen und Beschreibungen Conchylien, Vol. 2. *Littorina*, p. 139; used in combination *Fectaria pagodus*; error for *Tectarius* Valenciennes.
- 1858 *Hamus* 'Klein' H. & A. Adams, The Genera of Recent Mollusca, vol. 2, p. 656, refers to H. and A. Adams, 1854, vol. 1, p. 315; type-species here designated, *Hamus pagodus* (Linné) [= *Tectarius pagodus* (Linné)]; not *Hamus* 'Klein' R. B. Watson, 1886 [= Trochidae].
- 1899 *Echinellopsis* Rovereto, Atti della Societa Ligustica di Scienze naturali e geografiche, vol. 10, p. 109; new name for *Echinella* Swainson, 1840, not Bory St. Vincent, 1824.

Nomenclature—Due to similarities between the shells of *Tectarius* and some of the Trochidae, there has been a tendency for some of the former to be classified with the latter. This problem was discussed by Keen (1966) who recommended that the International Commission on Zoological Nomenclature validate *Tectarius* with the type-species *Tectarius coronatus* Valenciennes, [1832], i.e., in its accustomed sense. Her petition was granted in I.C.Z.N. Opinion 871 (Melville and China, 1969). It was assumed in this Opinion that the type-species of *Tectarius*, *T. coronatus* Valenciennes, is a synonym of *T. grandinatus* Gmelin. However, an examination of the type-specimen of *coronatus* in the Paris Museum shows it to be in actuality *T. rugosus* Wood, which usually has been erroneously referred to as *T. papillosus* Lamarck.

Another name which sometimes has been associated with *Tectarius* that has an exceedingly long and complicated history is the genus *Hamus*. It was mentioned originally by Klein (1753) where its use was of course pre-Linnaean. Bruguière (1792) gave a brief description, referring to Klein, but listed no species. Deshayes (1830)

declared it "a forgotten genus", indicating that he considered it unrecognizable. Mörch (1852) listed it, this time in the synonymy of *Littorina* Férussac, an invalid introduction (I.C.Z.N., Art. 11(d)). The first valid use of *Hamus* was not until H. & A. Adams (1858) used it as a senior synonym for *Tectarius* (see synonymy). It was later used by Wimmer (1880) and Watson (1886), the last being a taxon of Trochidae. I have designated as type-species of *Hamus* H. and A. Adams, 1858, *H. pagodus* (Linné) and consider this genus to be an absolute synonym of *Tectarius* Valenciennes.

The use of square brackets surrounding the date for *Tectarius* Valenciennes, [1832] is recommended by the International Code of Zoological Nomenclature in cases where the date of publication of a name has been determined on the basis of external evidence (I.C.Z.N. Recommendation 22A(3); also see Sherborn and Woodward, 1901; Keen, 1966; and Opinion 871).

***Tectarius rugosus* (Wood, 1828)**

(Pl. 388, figs. 10, 11)

Range—Philippines and Indonesia.

Remarks—The shells of well prepared and cleaned specimens of *Tectarius rugosus* tend to be quite colorful for Littorinidae, with the orange-pink coloration of the last two whorls contrasting with a purplish brown subsutural band. These colors do not show well in all specimens, however, and are not very visible in uncleaned specimens. The three large, non-umbilicate common species of the southwest Pacific may be distinguished by the number of major spiral rows of spines on the last whorl: 2 in *pagodus*; 3 in *tectumpersicum*; and 4 in *rugosus*. The closely-spaced stubby spines of *rugosus* also separate it from the other two. These characteristics do not of course help to distinguish it from *T. grandinatus*, but other characters and the Polynesian endemism of the latter are helpful in this case (see *Remarks* under *grandinatus*).

Habitat—Shore rocks and limestone cliffs 1-2 meters above high tide line (personal observations, Davao, Philippines, 1970).

Description—Shell reaching 39.7 mm (about 1½ inches) in length, broadly conical in shape, average obesity about .76 (51 specimens range from .68-.82); mature specimens moderately heavily constructed, imperforate, and sculptured on most postnuclear whorls with four, fairly closely-spaced rows of stubby, rounded, often slightly upturned spines. External color generally

yellowish white on early whorls, becoming pinkish orange on penultimate and body whorls; area of most posterior (subsutural) row of spines usually a contrasting purplish brown, and the same dark color may appear in lines and dashes inside outer lip of aperture; aperture tinted lighter pinkish orange. Base flattened, sculptured spirally with nodulose cords, a larger separate row just below periphery of body whorl. Whorls 6-8, flat-sided excepting spines. Length of spire usually greater than half the length of shell. Spire convex, produced at an angle of from about 60-67°. Aperture rounded-squarish; outer lip thickly produced in mature individuals, strongly plicate within; plicae not reaching edge of aperture; outer lip tapering to a thin, crenulate edge; inner lip smooth posteriorly, often stained a deeper orange than rest of aperture, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is the four spiral rows of spines. Spines not particularly aligned axially, although anteriormost 2 rows more so than others; from 17-23 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae. Posteriormost-but-one (3rd) row of

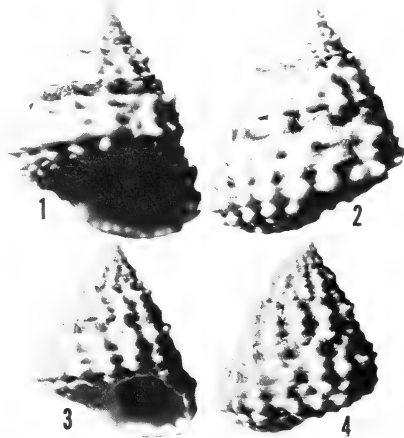


Plate 391. *Tectarius rugosus* (Wood, 1828).

Figs. 1, 2. *Turbo rugosus* Wood, lectotype, BM(NH) 1968370, 28.4 × 22.3 mm.

Figs. 3, 4. *Tectarius coronatus* Valenciennes, Holotype, MHNH ("Acapulco" [Luzon, Philippines]) 32.9 × 25.7 mm.

spines protrudes farthest on spire whorls, but this distinction largely lost on more mature whorls; posteriormost (4th) row of spines obscured by subsutural purplish brown color band especially on penultimate and body whorls. Secondary spiral sculpture, between each row of spines, consisting of raised cords, and overall spiral sculpture of microscopic threads. Axial sculpture consists of irregular flaky lines of growth. Operculum moderate in size, circular, an average one measuring about 7 mm. in diameter, thin, light-brown with a dark-brown center, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls at least partially decollate in all specimens examined, about 2, smooth, grayish white, first postnuclear whorls showing early signs of spiral striae and becoming nodulose. Radula littorinoid, 2-1-1-1-2; lateral tooth with a vertical partition and an embayment typical of Littorinidae. Animal moderately large, littorinoid; penis large, muscular and apparently highly extensible; seminal groove in deep fold running along medial edge to tip; tip vermiform, covered with papillae; lateral edge of penis supplied with large number of glands not extending onto vermiform tip. Reproductive data and life history unknown.

Measurements (mm) (all Philippines)—

length	width	No. whorls	locality
39.7	27.6	7+	Cadao Id., Naro Bay, Masbate
35.4	25.2	7+	Cadao Id., Naro Bay, Masbate
30.1	22.4	7+	San Miguel Bay, Ticao
25.9	21.2	8	Batag Id., Samar
23.9	16.3	7+	Bongao Channel, SW Sanga Sanga Id., Sulu Archipelago
21.0	15.3	7+	Borongan, E side Samar
17.5	13.7	7+	Papahag Id., Tawi Tawi Group
15.0	12.0	6+	Borongan Village, E side Samar
13.5	10.8	7+	Papahag Id., Tawi Tawi Group
12.6	9.8	6+	Papahag Id., Tawi Tawi
11.2	8.4	6+	Papahag Id., Tawi Tawi
8.4	6.8	5+	Papahag Id., Tawi Tawi

Synonymy—

- *Monodonta papillosa* of authors, not *M. papillosa* Lamarck, 1822 [= *Tectarius tectumperiscum* (Linné, 1758)].
- 1828 *Trochus rugosus* Wood. Supplement to the Index Testaceologicus or a Catalogue of Shells, British and Foreign, pl. 5, *Trochus*, fig. 7 (no locality given; Mindanao, Philippines, here selected); lectotype in BM(NH) 1968370, length 28.4 mm, width (ca.) 22.3; not *Litorina rugosa* Menke, 1843 [= *Nodilittorina australis* (Gray, 1826)].
- 1832 *Tectarius coronatus* Valenciennes in Humboldt and Bonpland, Voyage aux régions équinoxiales du Nouveau Continent, vol. 2, *Coquilles*, p. 271 (Acapulco [in error] locality here corrected to Luzon, Philippines); Holotype in MHNP.

1846 *Litorina papillosa elegans* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 140, *Litorina*, pl. 2, figs. 5, 7 (precise locality not given); figured specimens from Cuming Collection BM(NH) [not seen during 1968 visit] and Saul Collection, Cambridge Museum.

1846 *Litorina papillosa quadriseriata* Philippi, *ibid.*, p. 140, *Litorina*, pl. 2, fig. 2 (Zanzibar [in error] locality here corrected to Luzon, Philippines); type-specimen may be in BM(NH) [not seen during 1968 visit]; refers to "*Trochus rugosus* Wood Suppl. 1.5, f. 7".

Types—Although the name *T. papillosus* has been applied to this species (see Kaicher, 1956) the type-specimen of that species in the Geneva Museum is unquestionably *T. tectumperiscum* Linné, and *papillosus* is, therefore, an absolute synonym of *tectumperiscum* (q.v.). It also has been referred to as *Echinellopsis grandinatus* (Habe, 1961, p. 20; 1964, p. 28, both pl. 9, fig. 30) which is an error of nomenclature for *T. rugosus*. The first available name is *Trochus rugosus* Wood, 1828, the lectotype of which is in the BM(NH) 1968370. The holotype of *T. coronatus* Valenciennes is in the Paris Museum. The figured specimens of Philippi's *elegans* and *quadriseriata* may be in the BM(NH) and/or the Cambridge Museum. They were not discovered by me at the BM and may be lost. Philippi's figures are quite adequate for the interpretation of the species and may be considered as representative of the lectotypes: *elegans*, pl. 2, fig. 7; *quadriseriata*, pl. 2, fig. 2.

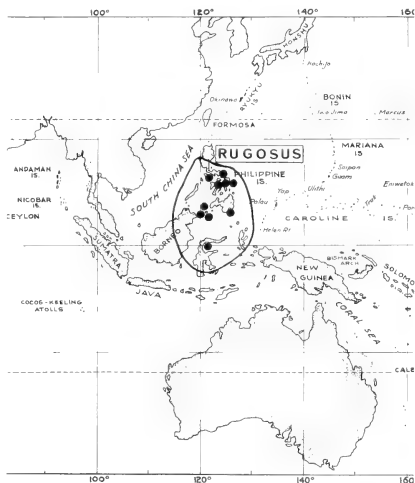


Plate 392. Geographic distribution of *Tectarius rugosus* (Wood) in the Philippines and Indonesia.

Records—PHILIPPINES: Port Galera, Mindoro; San Miguel Bay, Ticao Id.; Cado Id., Naro Bay, Masbate (all USNM); Borongan Village (USNM, Del. Mus. N.H., ANSP, MCZ); Batag Id., both Samar (USNM); Samal Id., Davao Bay (MCZ, USNM, WAM); Zamboanga, both Mindanao (ANSP, Del. Mus. N.H.); Jolo Id. (MCZ); Tabawan Id. (ANSP); Papahag Id. (USNM); Bongao Channel, SW Sanga Sanga Id., all Sulu Archipelago (ANSP). INDONESIA: Buka Buka Id., Gulf of Tomini, Celebes (USNM).

***Tectarius grandinatus* (Gmelin, 1791)**

(Pl. 388, figs. 1,2; pls. 393-395)

Range—The Cook, Society, Tuamotu and Gambier Islands, southeastern Polynesia.

Remarks—*Tectarius grandinatus*, an inhabitant of southeastern Polynesia, apparently is geographically isolated from the several other members of the genus *Tectarius* in the Indo-Pacific, the others being found in the East Indies. It is quite distinct, morphologically, from *pagodus* and *tectumpersicum*, but, interestingly, is very close in appearance to *T. rugosus* in general matters of sculpture and external anatomy of the animal. Superficially, *grandinatus* might be thought more closely related to *Cenchritis muricatus* (L.) of the western Atlantic. However, the radula, penial anatomy (Abbott, 1954) and a close examination of shell sculpture and structure causes me to reject that theory: *grandinatus* has not been observed to be umbilicate, while *muricatus* sometimes is; the aperture of *muricatus* is never thickened and plicate as it is in *grandinatus*; the operculum of *grandinatus* is rounded with the nucleus near the center, that of *muricatus* is more oval with the nucleus near the side.

The many similarities between *rugosus* and *grandinatus* together with their spatial isolation suggest the possibility that they may have evolved from the same species stock. Although a subspecific relationship may be indicated, the two are here considered to have developed full specific differentiation.

Habitat—Usually occurs on low islands within the geographic range; on coral reef flats near the high tide line, on jagged pieces of raised reef.

Description—Shell reaching 37.9 mm (about 1 1/2 inches) in length, elongate conical in shape, average obesity about .72 (44 specimens range from .62-.82); rather solidly and thickly constructed for its size, imperforate; mature specimens with very deeply impressed suture and rounded whorls; sculptured with four spiral rows per whorl of stubby spines. External shell color yellowish white; often coated with what appears

to be a light-yellow to brown or rather dark grayish brown periostracum which may wear thin especially at tips of spines; no definite color pattern apparent; occasional lines or splotches of medium brown present; upper (most posterior) part of aperture usually covered with a brown glaze. Base moderately flattened, sculptured spirally with nodulose cords. Whorls 7-9, moderately rounded. Length of spire usually considerably greater than half the length of shell. Spire convex, produced at an angle of from 58-60°. Aperture rounded; outer lip considerably thickened, plicate within, tapering to a thinner, crenulate edge. Inner lip with a thin, brown glaze posteriorly, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture often deeply impressed, typically forming a channel between whorls. Primary sculptural feature is the four spiral rows of spines. Spines not regularly aligned axially, although anteriormost two rows more-so than others; from about 17-25 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae; bases of posteriormost row of spines usually separate; second from anterior row usually the smallest. Secondary spiral sculpture be-

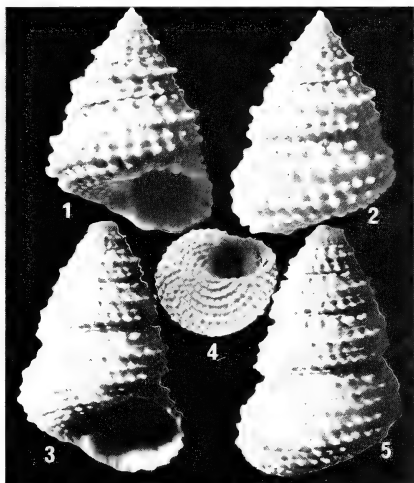


Plate 393. *Tectarius grandinatus* (Gmelin, 1791).

Figs. 1,2. *Trochus grandinatus* Gmelin, lectotype in ZMC, specimen figured by Chemnitz, Conchylien Cabinet, vol. 10, pl. 169, fig. 1639, from Palmerston Atoll, Cook Islands, 32 × 22.4 mm.

Figs. 3-5. *Monodonta coronaria* Lamarck, holotype, MHNG 1096/23, 41 × 27 mm.

tween rows of spines consisting of 2-4 raised cords; overall microscopic sculpture of fine, closely-spaced spiral threads. Axial sculpture consisting of fine, irregular, closely-spaced, overlapping lines of growth. Shell surface under high magnification may show minute closely-spaced perforations. Operculum moderate in size, rounded-oval, an average one measuring about 9 mm. in diameter, thin, light-brown with a dark-brown center, paucispinal, nucleus about central. A thin, light- to dark-brown periostracum present; closely applied but easily worn away; periostracum smooth and dully shining. Nuclear whorls about 1 1/2, smooth and shining; first post-nuclear whorl rapidly becoming multi-carinate and developing spines on the second. Radula littorinoid, 2-1-1-1-2; lateral tooth with a vertical partition and with an embayment characteristic of Littorinidae. Animal moderately large, littorinoid. Penis fairly large and apparently quite extensible; seminal groove in deep fold running along medial edge to tip and bordered by thickened, papillose glandular-appearing tissue; distal end of penis vermiform; lateral edge of penis lined with large number of glands not extending onto vermiform tip. Reproductive data and life history unknown.

Measurements (mm)—

length	width	no. whorls	locality
37.9	23.4	7+	Manihi, Tuamotu Ids.
34.3	21.5	7+	Aitutaki, Cook Ids.
32.0	22.8	6+	Mangaia, Cook Ids.
29.8	21.2	7+	Mangareva, Gambier Ids.
24.3	18.7	8+	Bird Id., Palmerston Atoll
22.0	17.0	9	Bird Id., Palmerston Atoll
20.7	15.7	7+	Cooks Motu, Palmerston Atoll
18.1	14.7	7+	Mangaia, Cook Ids.
16.1	13.2	6+	Aitutaki, Cook Ids.
14.3	10.8	6+	Aitutaki, Cook Ids.
12.4	9.1	9	Tikahau Atoll, Tuamotu Ids.
7.8	6.0	6+	Mangaia, Cook Ids.

Synonymy—

- [1784 *Trochus bullatus* Martyn, The Universal Conchologist, vol. 1, fig. 38; rejected work, I.C.Z.N. Opinion 456].
- 1791 *Trochus grandinatus* Gmelin, Systema Naturae, ed. 13, p. 3585 (ad Palmerstoni insulam [=Palmerston Atoll, Cook Islands]; refers to Chemnitz "Conch" vol. 10, p. 291, pl. 169, fig. 1639 and to Martyn "Conch", vol. 1, fig. 38. Lectotype, here selected, specimen from Spengler Collection, ZMC, figured by Chemnitz; see our pl. 393, figs. 1 and 2, 32 × 22.4 mm).
- 1816 *Monodonta coronaria* Lamarck, Liste Des Objets Représentés, Tableau Encyclopédique et Méthodique, part 23, p. 10, pl. 447, fig. 6 a,b (no locality given); Holotype MHNG 1096/23, 41 × 27 mm; 1822, Histoire Naturelle Des Animaux sans Vertèbres, vol. 7, p. 33.

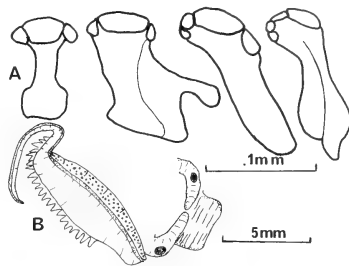


Plate 394. *Tectarius grandinatus* (Gmelin).

Fig. A. Radula.

Fig. B. Penis (both from Palmerston Atoll, Cook Islands, USNM 685165).

Types—The lectotype of *Trochus grandinatus* Gmelin, the specimen figured by Chemnitz, vol. 10, p. 291, pl. 169, fig. 1639, is in the Zoological Museum Copenhagen. It measures 32 × 22.4 mm (see pl. 393, figs. 1,2). The Holotype of *Monodonta coronaria* Lamarck is in the MHNG 1096/23 (see pl. 393, figs. 3-5). It measures 41 × 27 mm.

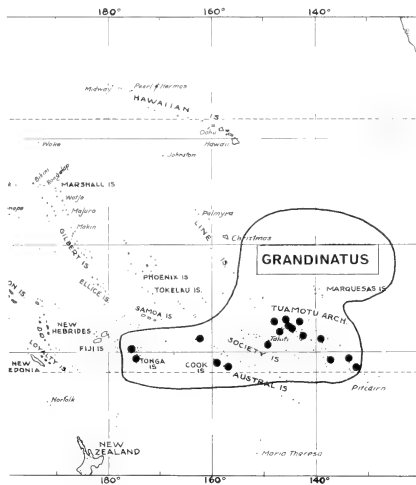


Plate 395. Geographic distribution of *Tectarius grandinatus* (Gmelin) in the southeastern Pacific Ocean.

Records—COOK ISLANDS: Palmerston Id.; Aitutaki (both USNM, ANSP, Del. Mus. N.H.); Hervey Ids. (USNM, MCZ, ANSP); E. side Koromiri Id., S.E. Rarotonga (ANSP); Mangaia (USNM); SOCIETY ISLANDS: W. coast Bora Bora (ANSP); Tahiti (USNM, MCZ, ANSP); TUAMOTU ISLANDS: Manihi Atoll (USNM); Takarua Atoll (ANSP); Maia Id., Tikehau Atoll (USNM); Aratika Atoll (ANSP); N. of Temao Harbor, Makatea Id. (USNM); Toau Atoll; Raroia Atoll; (all ANSP) Raraka Atoll (Del. Mus. N.H.); Fakarava Atoll; Makemo Atoll; Tatakoto Atoll; Anaa Atoll; Vahitahi Atoll; Nengonengo Atoll; Tureia Atoll (all USNM); Marutea Atoll, Acteon Group (ZMA). GAMBIE ISLANDS: Mangareva Id. (USNM, MCZ).

Tectarius pagodus (Linné, 1758)

(Pl. 388, figs. 5-7)

Range—From the Philippines, through the Western Pacific Arc to the Solomon Islands.

Remarks—The name applied by Linné to this species could not have been more appropriately descriptive as the shell with its usually upturned spines very much resembles an oriental turretted pagoda. As pointed out by Dodge (1959) there are a number of similarities between *T. pagodus* and *T. tectumpersicum*, both described by Linné. However *pagodus* reaches a larger size, $2\frac{1}{2}$ inches versus 1 inch, is proportionately broader and has more prominent spinose carinae than *tectumpersicum*. There is seldom any difficulty in separating these species with comparative material at hand.

The method of reproduction in *pagodus* remains to be observed. The normal habitat of the species is on cliffs above the sea. As there is no evidence that the species is ovoviparous, there must be a periodic migration to the sea for breeding purposes, although such a phenomenon has not been reported.

Another question arising from the high shore habitat of these nominally marine snails concerns their food. Rumphius (1705) early suggested that they feed upon the cliffs where they live. Examination of some fecal pellets of this species revealed the presence of considerable debris and what appeared to be plant cells. It is quite likely that *T. pagodus* feeds on plant life such as algae and lichens growing on the sea cliffs. The radula is extremely long which may denote such a browsing manner of feeding, the extra length possibly being required because aerial feeding without lubrication from sea water causes a rapid wearing of the teeth (see Quoy and Gaimard, Astrolabe, pl. 62, fig. 1).

Habitat—". . . these animals suck their food from the briny moisture of the cliffs to which they

cling, being unable to endure the water" (Rumphius, 1705, p. 74). Found on vertical limestone cliffs 1-2 meters above high tide line (personal observations, Moluccas Islands, Indonesia, 1970).

Description—Shell reaching 61.4 mm. (about $2\frac{1}{2}$ inches) in length, squatly conical in shape, average obesity about .93 (18 specimens range from .84-1.1); mature individuals rather heavily constructed, imperforate, and sculptured on the body whorl with 2 carinate rows of usually thick, straightly projecting or slightly upturned spines, between which spiral cords are roughly produced and the shell surface often thrown into oblique waves. Overall external color yellowish to grayish white, with no discernable pattern; in young specimens dark-brown spiral lines may be present externally or within aperture; aperture usually yellowish brown, its edge white. Base distinctly flattened, sculptured spirally with nodulose cords extending into aperture; base separated from upper part of body whorl by one of the rows of spines at periphery. Whorls 5-8, flat-sided, excepting spines. Length of spire usually greater than half the length of shell. Spire convex, produced at an angle, excepting spines, of from $55-65^\circ$. Aperture broadly rounded; outer lip thickly produced in mature individuals, strongly plicate within; plicae not reaching edge of aperture; inner lip smooth, white posteriorly, but forming a prominent tooth-like bulge anteriorly near junction with outer lip at base of columella. Suture somewhat obscure, marked by protrusion of secondary carinae of succeeding whorl. Outstanding sculptural feature is the midwhorl spinose carina, with typically from 9-12 antero-posteriorly flattened, triangular-shaped spines on carina of body whorl. Surface of shell at base of spines raised to form oblique fold often reaching to suture. Secondary spine bearing carinae at per-

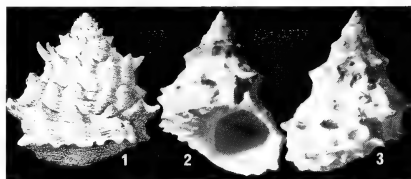


Plate 396. *Tectarius pagodus* (Linné, 1758).

Fig. 1. *Turbo pagodus* Linné; lectotype figure from Argenville, pl. 11, fig. a.

Figs. 2,3. *Monodonta bicolor* Lamarck, holotype, MHNG 1096/19, 54×38.2 mm.

iphery of each whorl, entirely visible only on body whorl and protruding above suture of preceding whorls. Secondary spiral sculpture of raised, roughened spiral cords in turn, covered with countless closely-spaced spiral microscopic textural threads. Operculum large (average about 16 mm. diameter) thin, brown, circular, corneous, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls partially decollate in all specimens examined, earliest whorl (probably first postnuclear) is spirally striate, the midwhorl carina beginning about second postnuclear whorl; carina becoming nodulose or prespinose almost immediately. Radula littorinoid (2-1-1-1-2) extremely long; lateral tooth partitioned and with an embayment. Animal large, also littorinoid; sides of foot and tentacles bright yellowish orange, remainder of animal grayish brown (color observations on living animals from Kai Islands, Moluccas, Indonesia); penis well-developed, with the seminal duct contained within a deep fold running along its medial edge; with a large number of glands attached along lateral edge; penis minutely papillose also over its surface, unbranched. Reproductive data and life history unknown.

Measurements (mm) (width includes spines)

length	width	no. whorls	locality
61.4	45.0	7+	Luttee, Choiseul Id., Solomon Islands
57.1	47.8	6+	Pavuvu Id., Russel Group, Solomon Islands
49.3	42.3	7+	Luttee, Choiseul Id., Solomon Islands
46.9	43.4	8+	Pavuvu Id., Russel Group, Solomon Islands
44.4	42.3	7+	Bougainville Id., Solomon Islands
41.3	37.4	5+	Majugag Id., W coast Buka Id., Solomon Islands
39.7	40.0	8	Luttee, Choiseul Id., Solomon Islands
31.5	31.9	6+	Balagnan Id., Surigao District, Mindanao, Philippines
27.5	25.5	8	Socipori Ids., Schouten Ids., West Irian
14.3	12.6	7	Biak, West Irian

Synonymy—

- 1758 *Turbo pagodus* Linné, *Systema Naturae*, ed. 10, p. 762; refers to Argenville, pl. 11, fig. A "Pagodus" [lectotype figure]; (type-locality, O. Asiatico, here restricted to Amboina, Moluccas).
- 1822 *Monodonta bicolor* Lamarck, *Animaux sans Vertèbres*, vol. 7, p. 31 (no locality); holotype in MHNG 1096/19, 54 × 38.2 mm.

1840 *Pagodella major* Swainson, *A Treatise on Malacology*, p. 351 (no locality given); refers to Chemnitz, pl. 163, figs. 1541, 1542 (specimen figured is lectotype, possibly in Copenhagen Museum).

1850 *Pagodus verus* J. E. Gray in M. E. Gray, *Figures of Molluscan Animals*, vol. 4, p. 78; refers to *Trochus pagodus* Quoy [and Gaimard, *Astrolabe*] pl. [62, not "82"], figs. 1-4; not *Littorina papillosa* var. *vera* Philippi, 1846 [= *Tectarius tectumperiscum* Linné].

Types—The location of Linné's type of *Turbo pagodus* is unknown, and Dance (1967) has pointed out that this species is missing from the Linnaean collection in London. In the absence of a type, one of the figures cited by Linné in connection with the original description is here

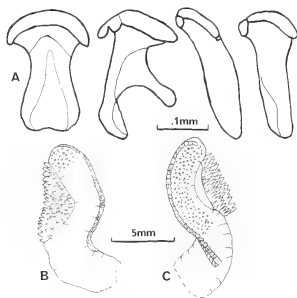


Plate 397. *Tectarius pagodus* (Linné).

Fig. A. Radula of specimen from West Irian; note smooth cusps probably denoting worn teeth, also "partitioned" lateral.

Fig. B. Penis, anterior, and C. posterior views respectively; note glands on lateral edge and papillose surface (both ANSP 207638).

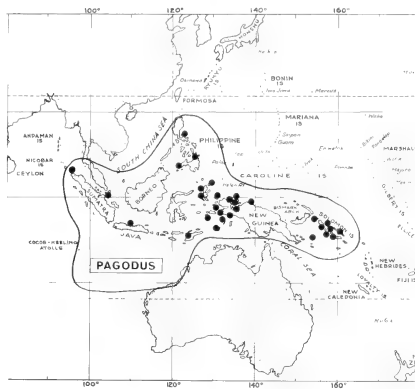


Plate 398. Geographic distribution of *Tectarius pagodus* (Linné) in the central Indo-Pacific faunal region.

designated as representing the lectotype: Argenville, pl. 11, fig. A. The type-locality, originally given as "O. Asiatico" is here restricted to Amboina, Moluccas. The holotype of *Monodonta bicolor* Lamarck is in the Museum d'Histoire Naturelle, Geneva (MHNG register no. 1096/19). The location of types of Swainsons' *Pagodella major* and of Gray's *Pagodus verus* are unknown to me, and the figures cited in connection with their descriptions may be considered as representing their lectotypes (see *Synonymy*).

Records—PHILIPPINES: E. coast Polillo (Del. Mus. N.H., USNM); Calapan, Mindoro Id. (Del. Mus. N.H.); Balagnan Id., Surigao District (USNM); Zamboanga, both Mindanao (ANSP Del. Mus. N.H.). INDONESIA: Pulau We, Sumatra (RNHL); Java (ANSP, RNHL); Timor (RNHL); Morotai Id.; Toetoe Id.; Dagaseli, both N Loloda Group (all MCZ); Ternate (RNHL); Buru Id. (ZMA); Ambon (MCZ, ZMA); Tanimbar Islands (RNHL); Kur Id.; Warbal Id., W of Nuhu Rowa, both Kai Ids. (both USNM, WAM); NEW GUINEA: Waigeo Id. (ANSP); Misool Id.; Fakfak (both Leiden); Manokwari (ANSP); Biak; Soepiori Id., both Schouten Ids. (both USNM); Rouw, Aorei Ids. (ANSP); Woodlark Id. (MCZ). SOLOMON ISLANDS: Majugag Id., W coast Buka Id.; Nr. Kihili, Buin, Bougainville Id. (both USNM); Choiseul Bay (ANSP); Lutee, both Choiseul Id. (ANSP, USNM); Ataa District, Malaita (ANSP); Roviana (MCZ); Pavuvu, Russell Group (USNM).

Tectarius tectumpersicum (Linné, 1758)

(Pl. 388, figs. 3,4)

Range—From the Philippines along the West-ern Pacific Arc through Melanesia.

Remarks—*Tectarius tectumpersicum* is grossly similar in many ways to *T. pagodus* and it often appears difficult to construct a point by point comparative description which clearly differentiates the two species except in matters of size and degree of obesity; *pagodus* reaches a length of 2½ inches (61 mm) while *tectumpersicum* rarely reaches 1½ inches (34 mm); *pagodus* is very obese, sometimes being wider than high, but in *tectumpersicum* the width of shell is generally only about 77% of the length. Differences are apparent also in spinosity, there being two rows of spines on the body whorl of *pagodus* and 3 rows in *tectumpersicum*. Spines in *tectumpersicum* tend to be stubby and round-ended while in *pagodus* they are pointed and broadly triangular, although there are occasional specimens of *tectumpersicum* which tend to resemble small, mature *pagodus*. Generally, however, specimens of *pagodus* the size of *tectumpersicum* are obviously immature and thin-lipped, so that the "rule-of-thumb" involving size of specimens can be depended on to separate the species.

Habitat—Lives in pockets of worn, raised limestone reef rock, 1-2 meters above high tide line (personal observations, Moluccas Islands, Indonesia, 1970).

Description—Shell reaching 34.6 mm (about 1⅞ inches) in length, conical in shape, average obesity about .77 (38 specimens range from .64–.85), mature individuals moderately thick in structure, imperforate, and sculptured with three main rows of stubby, often upturned, spines on body whorl, and usually with two rows on spire whorls, between which spiral cords are roughly produced, wavy or papillose and often approaching minor rows of spines. External color yellowish to grayish white, with no regular patterning although some specimens have diffuse dark spiral cord bands externally or within aperture especially at edge of outer lip or on tooth-like bulge of inner lip. Remainder of aperture usually white or yellowish white. Base moderately flattened,

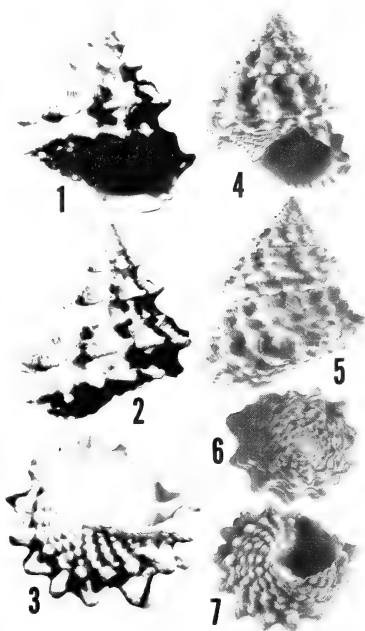


Plate. 399. *Tectarius tectumpersicum* (Linné, 1758).

Figs. 1-3. *Turbo tectumpersicum* Linné, lectotype in Linnean Society of London collection, ca. 25 × 23 mm.

Figs. 4-7. *Monodonta papillosa* Lamarck, lectotype, MHNG 1096/22-2, 29.3 × 25.5 mm.

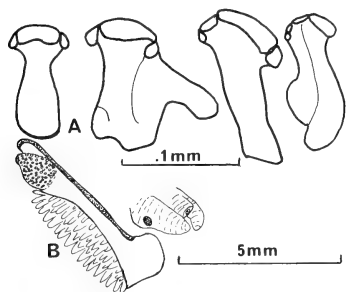
Plate 400. *Tectarius tectumersicum* (Linné).

Fig. A. Radula.

Fig. B. Penis (both from Biak, West Irian, ANSP 206421 and USNM 637390).

sculptured spirally with nodulose cords which may extend into aperture; base separated from upper part of body whorl by a row of spines at periphery. Whorls 6-8, rather flatsided excepting spines. Length of spire greater than half the length of shell. Spire convex, produced at an angle of from about 55-65°. Aperture compactly rounded; outer lip thickly produced; strongly plicate within, but thin and crenulate at apertural edge; inner lip smooth posteriorly, but forming a tooth-like bulge anteriorly near junction with outer lip at base of columella. Suture obscure, partially masked by lower row of spines at periphery of whorls. Center row usually bearing largest spines, from 9-12 on body whorl; the more posterior row, near suture has smaller spines but about same number; anterior row at periphery smaller still and more numerous with from 13-16 spines. On spire whorls center row of spines may predominate with others being either hidden or suppressed. Spines usually not aligned axially. Secondary spiral cords in some specimens almost as spinose as primary ones; in other specimens hardly noticeable. Entire surface covered with closely spaced spiral microscopic textural threads. Axial sculpture consists of often coarse, irregular lines of growth. Operculum moderate in size (average about 6-7 mm diameter), thin, brown, circular, corneous, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls about two, but at least partially decollate in all specimens examined; brown, smooth for at least 1 revolution, then becoming carinate; first post nuclear whorl weakly nodulose and rapidly becoming spinose. Radula littorinoid (2-1-1-1-2)

[teeth about $\frac{1}{2}$ the size of those of *T. pagodus*]; lateral tooth partitioned and with an embayment. Animal medium-sized, littorinoid; penis large, unbranched, with a large number of glands along lateral edge, $\frac{3}{4}$ the length to tip; surface of penis otherwise papillose; seminal duct deeply folded. Life history unknown.

Measurements (mm) (width includes spines)—

length	width	no. whorls	locality
34.6	24.5	6+	Pavuvu Id., Russell Group, Solomon Islands
31.4	23.3	8	Lunga, Guadalcanal, Solomon Islands
26.7	17.4	7+	Timor, Indonesia
22.8	18.4	6+	Cebu, Philippines
21.4	15.9	7+	Biak, West Irian
20.0	15.5	6+	Biak, West Irian
19.2	16.0	6+	Cebu, Philippines
18.1	13.7	7+	Biak, West Irian
15.2	12.9	6+	Anir Id., New Ireland
13.6	10.3	8	Philippines

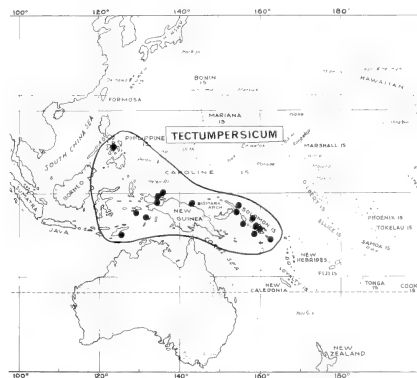
Synonymy—

1758 *Turbo tectumersicum* Linné, Systema Naturae, ed. 10, p. 762 (no locality given; Cebu Id., Philippines, here selected as type-locality); lectotype in Linnean Society of London collection.

— *Trochus bullatus* "Martyn" of authors; [not *T. bullatus* Martyn, 1784, Universal Conchologist, vol. 1, fig. 38; non-binomial; is *Tectarius grandinatus* (Gmelin, 1791)].

1822 *Monodonta papillosa* Lamarck, Histoire Naturelle des Animaux sans Vertèbres, vol. 7, p. 32. ("les mers de Timor"); lectotype MHNG 1096/22-2.

1846 *Litorina papillosa vera* Philippi, Abhandlungen und Beschreibungen Conchylien, vol. 2, p. 141 (no locality given); refers to "Delessert, Recueil, pl. 36, fig. 10," here selected as the lectotype figure.

Plate 401. Geographic distribution of *Tectarius tectumersicum* (Linné) in the central Indo-Pacific faunal region.

Types—The specimen of *Turbo tectumpersicum* Linné in the Linnaean shell collection located in the Linnean Society, London, may be considered the lectotype of this species; it measures approximately 25mm length (about 1 inch). The lectotype somewhat resembles *T. pagodus* but may be recognized by its rounded spines and the mature, thickened shell. The figure cited by Linné, "Argenville, pl. 11, fig. P", is controversial and a poor representation of the species (also see Dodge, 1959, p. 229). As no type-locality was given by Linné, Cebu Island, Philippines, is here selected as a place from which specimens could have come in the early 18th century. The figure referred to by Philippi, "Delessert, Recueil, pl. 36, fig. 10", is here selected as the lectotype figure of *Litorina papillosa vera*. The lectotype of *Monodonta papillosa* Lamarck, which proves to be an absolute synonym of *T. tectumpersicum* is in the Geneva Museum (MHNG 1096/22-2; see our pl. 399 figs. 4-7).

Nomenclature—The name *tectumpersicum* does not need to agree in gender with *Tectarius* because the former is a noun in apposition, meaning "persian roof".

Records—PHILIPPINES: Cebu (USNM). INDONESIA: Timor (USNM, RNHL); Ambon; Kur Id.; Warbal Id., W of Nulu Rowa, both Kai Islands (all USNM, WAM). NEW GUINEA: Wasior, Wandammen Bay (ZMA); Soepiori Id., (MCZ); Biak Id., both Schouten Islands, all West Irian (USNM); reef at Cape Moem, nr. Wewak, Territory of New Guinea (MCZ). BISMARCK ARCHIPELAGO: Feni Ids., E of New Ireland (USNM). SOLOMON ISLANDS: Nissan Id., Green Islands (SMF); Choiseul Bay, Choiseul Id. (ANSP); Stirling Isle, Treasury Ids.; Munda, New Georgia; Pavuvu Id., Russell Group; Lunga, Guadalcanal (all USNM); Santa Ana Id., S. of San Cristobal (ANSP).

Tectarius rusticus (Philippi, 1846)

(Pl. 388, figs. 8, 9; pls. 402, 403)

Range—Northern Western Australia.

Remarks—This species is restricted to northern Western Australia according to available locality data. It appears to be most closely related to *T. rugosus* from which it differs in its usually less regularly sculptured, more flat-sided whorls and in its lack of external coloration. In *T. rusticus* the subsutural, midwhorl and peripheral rows of spines are quite commonly strongly expressed, while in *rugosus* all rows are subequal.

Habitat—Lives on rocks above high tide line.

Description—Shell reaching about 40 mm (about 1½ inches) in length, broadly conical in shape, average obesity about .77-.29 specimens range from .72-.83; becoming moderately thick

in structure, imperforate, and sculptured with 2-3 main rows per whorl of rather muted spines. External color yellowish white with occasional faint orange stripes; inside of aperture white and occasionally tinged with pinkish orange, often with brown lines at its edge and revolving within; apertural tooth often stained with brown. Base flattened, sculptured spirally with nodulose cords, the strongest of which occurs just below periphery of body whorl. Whorls 6-8, rather flat sided. Length of spire greater than half the length

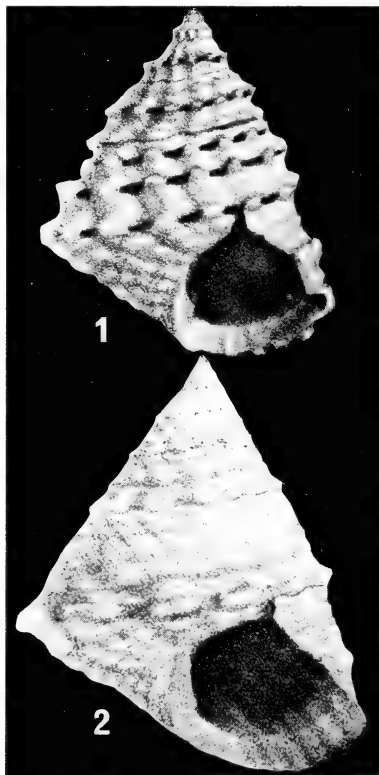


Plate 402. *Tectarius rusticus* (Philippi, 1846).

Figs. 1,2. *Litorina papillosa rustica* Philippi, knobby and smooth forms, respectively.

Fig. 2 (lectotype figure) probably is representation of Philippi's concept of *L. p. subinermis*, the smooth form; both from Point Swan, northern Western Australia; from *Abbildungen und Beschreibungen Conchylien*, vol. 2, *Litorina*, pl. 2, figs. 3,4.

of shell or the two may be about subequal. Spire convex, produced at an angle of about 68° . Aperture rounded to squarish; outer lip thickly produced, internal pliae only moderately produced and not reaching edge of aperture; outer lip tapering to thin crenulate edge; inner lip forming a tooth-like bulge anteriorly near junction with outer lip; tooth often stained with brown. Suture usually obscured by anteriormost row of spines of preceding whorl. Spiral spinose sculpture subdued, usually three rows are outstanding: the anteriormost, posteriormost and central rows of each whorl, the rest being limited to undulating, slightly bumpy cords; from 12-14 spines per row on body whorl; spines sometimes coalesce into oblique axial bars. Fine sculpture composed of microscopic wavy spiral cords and finer threads. Operculum moderate in size, circular, light-brown with a dark-brown center, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls partly decollate in all specimens examined; remaining portions smooth, white; early postnuclear whorls rapidly becoming spirally striate. Radula littorinoid, 2-1-1-1-2, similar in appearance to that of *T. rugosus*. Preserved specimens not available for observations on anatomy; radula obtained from dried specimen. Nothing reported concerning reproduction and development.

Measurements (mm) (all Western Australia)—

length	width	no. whorls	locality
35.5	29.0	5+	Yampi Sound, W.A.
34.5	27.5	6+	Cliff Id., King Sound
32.4	23.3	8+	Buccaneer Archipelago
25.8	20.6	7+	Buccaneer Archipelago
23.2	18.8	5+	Cliff Id., King Sound
22.1	17.1	6+	Buccaneer Archipelago
21.9	16.2	7+	Buccaneer Archipelago
21.1	15.3	7+	Cliff Id., King Sound
16.3	12.7	6+	Buccaneer Archipelago
15.8	12.2	6+	Buccaneer Archipelago

Synonymy—

- 1846 *Litorina papillosa rustica* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, *Litorina*, p. 140, pl. 2, fig. 3 [and 4 Lectotype Figure] (Point Swan [Cape Leveque, Dampier Land, northern Western Australia]; type-specimen may be in Berlin Museum).
- 1846 *Litorina papillosa subinermis* Philippi, *ibid.*, p. 141, pl. 2, fig. 4.
- 1857 *Littorina bullata* in Reeve, Conchologia Iconica, vol. 10, *Littorina*, pl. 1, fig. 1c; not *Trochus bullatus* Martyn [non-binomial] which is *Tectarius grandinatus* Gmelin.
- 1971 *Tectarius pagodus* Linnaeus, Wilson and Gillett, Australian Shells, p. 30, pl. 11, fig. 9.

Records—WESTERN AUSTRALIA: Troughton Islands, N. of Admiralty Gulf; S.E. Wood Island, E. of Cockatoo Island; Yampi Sound; Koolan Island (all WAM); Kellan Island, Buccaneer Archipelago (AMS; USNM; MCZ); Cliff Island (USNM) all vicinity of King Sound.



Plate 403. Geographic distribution of *Tectarius rusticus* (Philippi) in northern Western Australia.

Tectarius songoense (Martin, 1931)

(Pl. 404, figs. 3,4)

Range—Eocene of Java, Nanggoelan-beds, Kali Songo.

Remarks—It is not too difficult to determine from Martin's illustration just why he assigned this species to "*Tectarium*". There is a weakly nodulose sculpture, perhaps better described as beaded, and there appears to be a columellar tooth, a structure characteristic of Tectariinae. The general shape and appearance are, however, more suggestive of Trochidae. The species is tentatively here placed in the subfamily Tectariinae for want of positive proof to the contrary.

Synonymy—

- 1931 *Tectarium* (*Echinella*) *songoense* K. Martin, Wetenschappelijke Mededeelingen Dienst Mijnbouw, no. 18, p. 41, pl. 6, fig. 5, 5a, (Upper Eocene, Nanggoelanbeds, Java); unique holotype probably in Geological Museum, Leiden; length 8 mm.

Subgenus *Subditotectarius* Ladd, 1966

Type: *Tectarius rehderi* Ladd, 1966

Small, stout; spire conical, base convex; with beaded spiral ribs and slightly oblique axial lines; aperture strongly plicate within. Sculpture subdued, consisting of small beads formed by convergence of axial growth lines and spiral threads.

Synonymy—

1966 *Subditotectarius* Ladd, Geological Survey Professional Paper 531, p. 59, type-species by original designation: *Tectarius rehderi* Ladd.

Tectarius (Subditotectarius) rehderi Ladd, 1966

(Pl. 404, figs. 5-7)

Range—Lower Miocene, Marshall Islands.

Remarks—The fossil *Subditotectarius rehderi* is characterized by its subdued beaded sculpture as compared with *Tectarius s.s.* with its larger nodules and spines. Otherwise the species is quite similar to other *Tectarius* in outline and sculpture, and in the presence of a columellar tooth and plications within the aperture. Although apparently clearly a tectariine *S. rehderi* is not believed to be closely related to any living species.

Synonymy—

1966 *Tectarius (Subditotectarius) rehderi* Ladd, Geological Survey Professional Paper 531, p. 59, pl. 11, figs. 11-13 (drill hole 2A, Bikini Atoll, 1,051-1,057 feet; early miocene); holotype USNM 648342, 2.8×2.4mm.

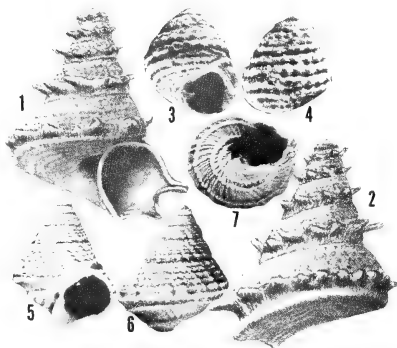


Plate 404. Fossils of Tectariinae and Echinininae.

Figs. 1,2. *Echininus adelaidensis* (Cotton, 1947) holotype, 16 × 12 mm.

Figs. 3,4. *Tectarius songoense* Martin, 1931; holotype, 8 mm length.

Figs. 5-7. *Tectarius rehderi* Ladd, 1966, holotype, 2.8 × 2.4 mm.

Subfamily Echinininae, new subfamily

Genus *Echininus* Clench and Abbott, 1942Type: *Echininus cumingi* (Philippi, 1846)

The genus *Echininus sensu lato* includes the nominate subgenus, *Echininus*, typified by the umbilicate and spinose *E. cumingi* and also *E. cumingi spinulosus*, both of the western Pacific, and the subgenus *Tectininus* Clench and Abbott, 1942, having the non-umbilicate and less spinose monotype, *E. (T.) nodulosus* (Pfeiffer), a species which inhabits the Caribbean area. Members of both subgenera have what may be called multispiral (polygyrous spiral type) opercula and possess moderately spinose shells. In *Echininus sensu stricto* the central radula tooth is moderately reduced in width, while in *Tectininus* it is dramatically reduced and narrowed. Abbott (1954) discussed the phylogenetic position of *Echininus* and concluded that it belongs in Littorinidae although it possesses many specialized characters such as the multispiral operculum, an umbilicus and a narrow central radula tooth. As there are no representatives of *Tectininus* in the Indo-Pacific, only *Echininus s.s.* will be considered here.

Synonymy—

- 1854 *Echinella* 'Swainson' H. and A. Adams, The Genera of Recent Mollusca, vol. 1, p. 316; three species mentioned: *coronaria* Lamarck [= *Tectarius grandinatus* Gmelin]; *granulata* Swainson [unrecognizable]; and the exemplary species, *cumingii* Philippi; 1895, Pilsbry, Catalogue of the Marine Mollusks of Japan, p. 175; 1901, Pilsbry, Proceedings of the Academy of Natural Sciences of Philadelphia, p. 198; 1903, Kesteven, Proceedings of the Linnean Society of New South Wales, for 1902, part 4, p. 632, in part; not *Echinella* Swainson, 1840 [= *Tectarius s.s.*].
- 1942 *Echininus* Clench and Abbott, Johnsonia, vol. 1, no. 4, p. 3; new name for *Nina* Gray, 1850, Figures of Molluscos Animals, London, vol. 4, p. 78; Type species by monotypy *Trochus cumingii* Philippi; not *Nina* Horsfield, 1829, nor Gray, 1855.

Subgenus *Echininus s.s.*

Pyramidal, umbilicate littorinids with a strongly spinose shell. In males the penis has a deep but open sperm duct, and basal penial glands are present. Operculum multispiral. Radula littorinoid, the central tooth moderately narrow.

Echininus cumingi cumingi (Philippi, 1846)

(Pl. 388, figs. 12, 13)

Range—From the Philippines along the western Pacific arc to New Hebrides and the Cook Islands.

Remarks—At first examination one finds it surprising that "*Cuming's Echininus*" is included in the Littorinidae. This species has many of the attributes of certain other families, perhaps resembling most some members of the family Trochidae with its conical shape, multispiral operculum and well-defined umbilicus. Animal characters, especially the radula, and gross reproductive features leave no doubt, however, that *E. cumingi* is a littorinid. Its closest relative is the smaller and less spinose, but otherwise very similar appearing subspecies, *E. cumingi spinulosus* (Philippi). The next most closely related and only other species in the subfamily, the Western Atlantic *E. (Tectininus) nodulosus* (Pfeiffer) differs in never being umbilicate and in having a considerably more reduced radula. The open condition of the spines occurs occasionally in *E. nodulosus* and their arrangement or alignment is similar. Both have multispiral opercula. Penial anatomy differs, however, *E. cumingi* having a cluster of basal penial glands, whereas *E. nodulosus* displays a basal swelling and a single gland located one half to two thirds the distance to the tip (see Abbott, 1954, fig. 55, p.q).

Habitat—Lives in pockets of weathered, raised limestone reef, 3-7 meters above high tide line (personal observations in Davao, Philippines and Moluccas Islands, 1970).

Description—Shell reaching 20.4 mm (about 3/4 inch) in length, broadly conical in shape, with

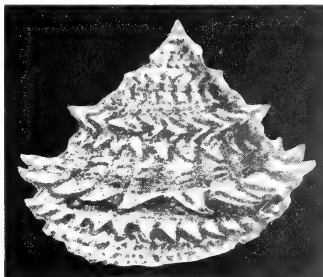


Plate 405. *Echininus cumingi cumingi* (Philippi, 1846). *Trochus cumingii* Philippi, lectotype figure of specimen in BM(NH), from Reeve, 1857, Conchologia Iconica, vol. 10, Littorina, pl. 2, fig. 8.

projecting spines, average obesity about .88 (33 specimens range from .77 to 1.03) only moderately thick in structure, umbilicate; suture impressed, whorls slightly rounded; sculptured with three rows of short, projecting, often unclosed spines. External shell color grayish tan, the spines often being reddish brown; a thin grayish brown periostrial coating apparent; aperture a diffuse yellowish to reddish brown, occasionally with three reddish brown color bands reflecting the position of the external spines. Base distinctly flattened, spirally sculptured with nodulose cords of which about the third below the periphery is the strongest. Umbilicus very deep but narrow in mature specimens; bordered medially by a rim of the columellar callus and distally by a basal fold. Whorls 6-8, only slightly rounded. Length of spire greater than half the length of the shell. Spire convex, produced at an angle of from about 66-76°. Aperture rounded, outer lip only moderately thickened, smooth within, the edge often undulating in the vicinity of the rows of spines; inner lip curved and shining, edentulous. Suture usually somewhat obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is the three spiral rows of spines. Posteriormost row of spines consisting of low, rounded protuberances; anteriormost row small, unclosed, moderately projecting, narrow-hoodlike and closely spaced; middle row of spines largest, most projecting, also incompletely closed. Rows of spines not aligned axially; spine count as follows: anterior row, 18-25; middle row, 14-17; posterior 15-16 (approximate range). Secondary spiral sculpture between rows of spines consists of from 4-6 slightly raised cords; overall microscopical spiral sculpture of fine, closely spaced threads. Axial sculpture consists of fine irregular often overlapping lines of growth. Operculum moderate in size, multispiral (polygyrous spiral type) having about 5-7 volutions, chitinous, dark-brown (pl. 389). Nuclear whorls smooth, light brown, shining, about 1.5 volutions; postnuclear whorls rapidly becoming striately sculptured and then spinose. Radula littorinoid, 2-1-1-1-2, central tooth very narrow, rather simple; lateral tooth only moderately narrow and with a well developed littorinoid notch.

Animal littorinoid; penis large and well-developed, with a bulbous swelling at its base; distal extremity simple; with as many as 12 penial glands clumped mostly on posterior surface near junction of bulbous base and extremity; sperm

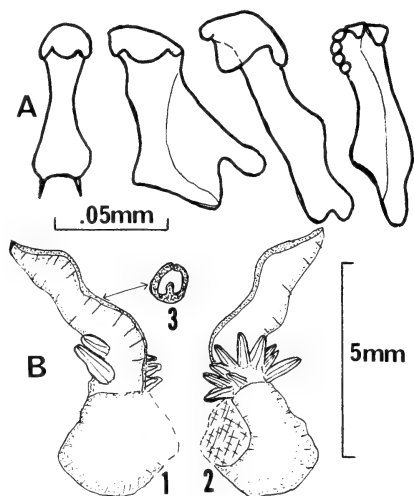


Plate 406. *Echininus cumingi* (Philippi).

Fig. A. Radula; note "spurs" on central tooth, and generally narrow dentition.

Fig. B. Penis. 1, anterior, 2, posterior, 3, cross-section of seminal groove; note cluster of glands near bulbous base (both from Davao Gulf, Mindanao, Philippines).

groove deeply folded, with an apparent internal fold best seen distally. Details of reproduction and life history unknown.

Measurements (mm)—

length	width	no. whorls	locality
20.4	17.3	7	Cook Islands
19.5	17.6	8	Philippines
18.5	14.9	7+	Stirling Isle, Treasury Ids., Solomon
17.5	14.3	7+	Stirling Isle, Treasury Ids., Solomon
17.0	14.9	7	Cook Islands
16.7	15.3	7+	Cook Islands
16.3	14.8	7+	Stirling Isle, Treasury Ids., Solomon
15.9	12.3	7+	Stirling Isle, Treasury Ids., Solomon
15.1	13.0	7+	Tana, New Hebrides
14.6	13.7	6+	Stirling Isle, Treasury Ids., Solomon
13.2	11.9	7+	Stirling Isle, Treasury Ids., Solomon
10.6	10.9	8	Philippines

Synonymy—

- 1846 *Trochus cumingii* Philippi, Proceedings of the Zoological Society of London, for 1845, p. 138 (Guimaras Id. [south of Panay Id.] Philippines; as *Littorina*, 1847, *Abbildungen und Beschreibungen Conchylien*, vol. 3,

Littorina, p. 53, pl. 6, fig. 22; lectotype in BM (NH), figured by Reeve, 1857, *Conchologia Iconica*, vol. 10 *Littorina*, pl. 2, fig. 8.

- 1879 *Trochus echinulatus* 'Kiener' in P. Fischer, *Spécies Général et Iconographie des Coquilles Vivantes*, pl. 43, fig. 2 [name and figure only]; *ibid.*, p. 459, places name in synonymy of *Tectarius cumingi* (sic); not *Trochus echinulatus* A. Alth, 1850.

Records—PHILIPPINES: Samal Id., Davao Bay, Mindanao (USNM, MCZ). INDONESIA: Karakelong Id., Talaud Ids. (MCZ); N. shore Warbal Id., W of Nuhu Rowa, Kai Ids.; W. side Mitak Id., Jamdena Strait, Tanimbar, both Moluccas (USNM, WAM). NEW GUINEA: Misool; Fakfak (both RNHL); Louisade Ids. (RNHL, NMW, ANSP). SOLOMONS: Stirling Isle, Treasury Ids., (USNM); Santa Ana (ANSP). NEW HEBRIDES: S end Black Beach, Tana (USNM). COOK ISLANDS: Mauke, Hervey Ids.; Rarotonga (both ANSP); Mangaia (USNM).

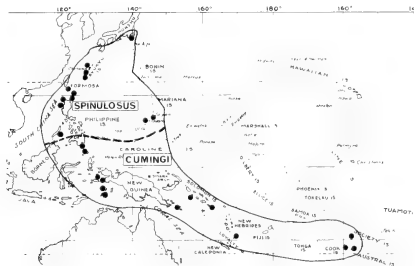


Plate 407. Geographic distribution of *Echininus cumingi* (Philippi) in the East Indies and Pacific Ocean, and of its more northerly distributed subspecies *E. cumingi spinulosus* (Philippi).

Echininus cumingi spinulosus (Philippi, 1847)

(Pl. 358, figs. 14, 15; pls. 407, 408)

Range—From southern Japan through the Ryukyu Islands, the northern and western Philippines and eastward to the Mariana Islands.

Remarks—*Echininus spinulosus* is very close in its relationship to *E. cumingi*, the differences between the two being more of degree than of kind. The two are apparently geographically isolated, or at least they occupy separate ranges and so the phenotypic differences may be ecologically influenced as well as having a genetic basis. Whatever the basis for the differences between them, it seems appropriate to consider them as subspecies. *Echininus spinulosus* never reaches as large a size or achieves the squatly conical shape of *E. cumingi*, and although the sculpture of the two is basically very similar, *cumingi* is always more distinctly spinose. Both are usually umbilicate although *spinulosus* is often narrowly

so and young specimens may lack this feature entirely, as did Philippi's type-specimen.

It is interesting to note that *E. luchuana* was described by Pilsbry (1901) as a subspecies of *cumingi*, which has caused some confusion. Some malacologists have continued to use the combination *E. cumingi luchuana* or simply *E. cumingi* when referring to the entity *E. spinulosus* (Kira, 1959, 1962; Habe, 1951). Philippi's figures (1847) clearly show the species concepts he intended: *E. spinulosus* (fig. 24), the smaller less pronouncedly spinose species (which includes *luchuana* as a synonym) and *E. cumingi* (fig. 22), the larger and more outstandingly spinose and more squatly conical species.

Habitat—On rocks above the high tide line.

Description—Shell reaching 16.8 mm (about $\frac{5}{8}$ inch in length, turbinate in shape, with short spines; average obesity about .84 (32 specimens range from .74-1.08) moderately thick in structure, mature specimens usually umbilicate; suture evident although often obscure; whorls moderately rounded; sculptured with three major rows of short spines per whorl. External shell color grayish to tannish orange, the short spines usually appearing whitish; apertural coloration

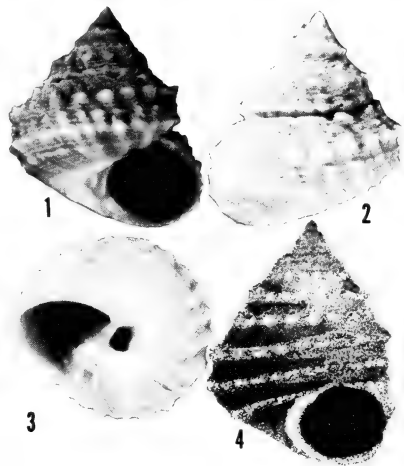


Plate 408. *Echininus cumingi spinulosus* (Philippi, 1847)

Figs. 1-3. *Echinella cumingi luchuana* Pilsbry, lectotype, ANSP 70962, 16 x 14 mm.

Fig. 4. *Littorina spinulosa* Philippi, lectotype figure, from *Abbildungen und Beschreibungen Conchylien*, vol. 3, *Littorina*, pl. 6, fig. 24.

tannish to brownish orange, occasionally with 3-4 darker brown color bands revolving within. Base moderately flattened, sculptured with nodulose cords of which about the third below the periphery is the strongest. Umbilicus usually rather narrow and occasionally absent, bordered medially by a rim of the columella callus and distally by a poorly to well defined basal fold. Whorls 6-8, only moderately well rounded. Length of spire greater than half the length of the shell. Spire convex, produced at an angle of from about 63-68°. Aperture rounded-oval, outer lip thin to only moderately thickened, smooth within, and often slightly undulating in vicinity of external spine rows; inner lip curved and shining, edentulous. Suture fairly evident to somewhat obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is three spiral rows of spines located centrally, anteriorly and posteriorly on each whorl; spiral cords between main rows tending to become nodular to spinose. Rows of spines not well aligned axially; spine count as follows: anterior row about 24; middle row about 19-23; posterior row about 16-19. Secondary sculpture consisting of 4-5 rows of spiral cords which occasionally become nearly as strongly spinose as the 3 primary rows which they separate; overall microscopical spiral sculpture of fine, closely-spaced threads. Axial sculpture consists of fine irregular lines of growth. Operculum small to moderate in size, multispiral (polygyrous spiral type) having 5-6 volutions, chitinous, dark brown. Nuclear whorls smooth, tannish white, shining, about 1.5 volutions; postnuclear whorls rapidly becoming striated and nodulose. Radula littorinoid, 2-1-1-1-2; central tooth narrow and reduced; lateral tooth with a distinct littorinoid notch. Animal littorinoid; penis unbranched; a well developed sperm groove running along its medial edge; distal portion papillose; 2-3 penial glands located half-way between base and tip in preserved specimen. Nothing has been reported concerning reproduction and life history.

Measurements (mm)—

length	width	no. whorls	locality
16.8	11.7	8	Fuga Id., Philippines
15.6	12.2	7+	"Japan"
14.9	11.1	7+	Yokohama, Japan
14.2	11.8	7	Batan Id., Philippines
13.9	11.5	6+	Batan Id., Philippines
13.5	10.9	8	Batan Id., Philippines
13.0	10.4	7	Kume-shima, Ryukyu Ids.
12.6	10.4	6+	Okinawa, Ryukyu Ids.

12.0	10.0	7+	Batan Id., Philippines
11.1	9.0	7	Batan Id., Philippines
10.8	10.5	7	Batan Id., Philippines
7.3	7.9	6	Batan Id., Philippines

Synonymy—

- 1847 *Litorina spinulosa* Philippi, *Abbildungen und Beschreibungen Conchylien*, vol. 3, *Litorina*, p. 53, pl. 6, fig. 24. Lectotype Figure (Manila); type may be in Berlin Museum.
- 1895 *Echinella cumingi* Phil. in Pilsbry, *Catalogue of the Marine Mollusks of Japan*, published by Frederick Stearns, Detroit, p. 175 (Yaeyama [Okinawa]).
- 1901 *Echinella cumingi luchuana* Pilsbry, *Proceedings of the Academy of Natural Sciences of Philadelphia*, p. 198 (Loo Choo Islands [Ryukyu Islands]); *ibid.* p. 394, pl. 19, fig. 16; lectotype ANSP 70962, ca. 16 × 14 mm.

Records—JAPAN: Yokohama (USNM). RYUKYU ISLANDS: Kadena Circle (USNM); Tsukin-shima, both Okinawa (MCZ); Kume-shima (MCZ ANSP, USNM, BPBM); Karimata, Miyako-shima (MCZ, ANSP); Ora Wan (USNM). TAIWAN: Hung-tou Hsu, off Pacific Coast (ANSP, USNM). PHILIPPINES: Santa Domingo de Basco, Batan, Batan Ids. (USNM); Dalupiri Id. (MCZ); Fuga Id., both Babuyan Ids. (USNM); Camp Wallace, Province of La Union, Luzon; Puerto Princessa, Palawan (both ANSP). MARIANA ISLANDS: Saipan; Piti Bay, Guam (both ANSP); Apra Bay; Asan Point, both Guam (both USNM).

Echininus adelaidensis (Cotton, 1947)

(Pl. 404, figs. 1,2)

Range—Adelaidean (Pliocene), South Australia.

Remarks—*Echininus adelaidensis* certainly is a unique appearing species which somewhat resembles certain of the Trochidae nearly as much as it does *Echininus* (cf. *Turcica* A. Adams or *Perrinia* H. and A. Adams, as shown in Wenz, 1938). The characteristics of its partly open spires and the presence of an umbilicus may be sufficient to relate it to *Echininus*, however. Cotton refers to *E. cumingi* Philippi having been collected in Caloundra, Queensland and Western Australia, but I have not seen such records in the course of the present study. It is possible that northern portions of Australia may be within the range of *E. cumingi* which reaches the southern Moluccas and New Guinea.

Synonymy—

- 1947 *Nina adelaidensis* Cotton, *Records of the South Australian Museum*, vol. 8, no. 4, p. 666, pl. 21, figs. 17, 18 (Adelaidean Pliocene, Salisbury Bore, 350 feet); holotype in Tate Museum, University of Adelaide, 16 × 12 mm.

"Littorina" incisa Yokoyama, 1927

(Pl. 358, figs. 4, 5)

Range—Pliocene of Japan.

- ★ *Remarks*—As pointed out by Habe (*in litt.*, 1971), this 5 mm. shell is a member of the Pyramidellidae. We erroneously considered it to be a *Littorina* (*Littorinopsis*) in our last number of Indo-Pacific Mollusca, vol. 2, no. 11, p. 466 [p. 05-340], pl. 358, figs. 4, 5.

Synonymy—

- 1927 *Littorina incisa* Yokoyama, Journal of the Faculty of Science, Imperial University of Tokyo, section II, Geology, Mineralogy, Geography, Seismology, vol. 2, part 4, p. 175, pl. 47, fig. 8 (Pliocene, Nagaya, Kaga, Japan); holotype in Geological Institute, Imperial University of Tokyo: 5 × 2.5 mm.
- 1970 *Littorina incisa* Yokoyama, Rosewater, Indo-Pacific Mollusca, vol. 2, no. 11, p. 466.

Littorina kozaiensis Nomura and Onisi, 1940

(Pl. 349, figs. 6, 7)

Range—Lower Miocene of Japan.

Remarks—This species was described as resembling *L. adonis* Yokoyama (see below), but as having a larger number of spiral grooves. The unique holotype (pl. 349, figs. 6, 7, a copy of the original illustration) offers little basis for comparison with Recent species.

Synonymy—

- 1940 *Littorina kozaiensis* Nomura and Onisi, Japanese Journal of Geology and Geography, vol. 17, nos. 3 and 4, p. 191, pl. 19, fig 6 a,b. (Yōsuibori, Simizu, Kozaimura, Japan); holotype: Saitō Hō-on Kai Museum, Register No. 21762; 11 × 8 mm.

Littorina adonis Yokoyama, 1927

(Pl. 349, figs. 8, 9)

Range—Pliocene of Japan.

Remarks—Placed provisionally here in the subgenus *Littoraria*, this species resembles *L. undulata*, although the strong spiral sculpture is also reminiscent of *Littorinopsis*, i.e. *L. scabra*, etc. Unfortunately the outer lip and a portion of the body whorl of the type (pl. 349, figs. 8, 9) are missing and it is difficult to be sure of their exact shape.

Synonymy—

- 1927 *Littorina adonis* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 8. (Upper Musashino, Koyasu southern Musashi, Japan); (unique holotype in collection of Geological Institute Imperial University of Tokyo: 6 × 4 mm.).

Littorina lucida Yokoyama, 1927

(Pl. 349, figs. 4, 5)

Range—Pliocene of Japan.

Remarks—This species is from the same deposit as *L. adonis* but lacks the deeply incised spiral sculpture. The type of *lucida*, although of approximately the same size as *adonis* is more slender.

We overlooked the fact that Habe, 1942 (Venus, vol. 12, p. 37) and Abbott, 1958 (Proc. Acad. Nat. Sci. Phila., vol. 110, p. 270) had pointed out that *L. lucida* was a synonym of *Assiminea japonica* von Martens, 1877. ★

Synonymy—

- 1927 *Littorina lucida* Yokoyama, Journal of the Faculty of Science Imperial University of Tokyo, section 2, vol. 1, part 10, p. 451, pl. 51, fig. 9 (Upper Musashino, Koyasu southern Musashi, Japan; unique holotype in collection of Geological Institute Imperial University of Tokyo: 5 × 3 mm.).

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

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THE GENUS *DRUPA* IN THE INDO-PACIFIC

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and

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Abstract

A revised classification of the gastropod genus *Drupa* Röding (Muricidae: Thaidinae) is presented. The following taxa are recognized: *Drupa* (*Drupa*) *morum morum* Röding, 1798; *D. (D.) morum iodostoma* (Lesson, 1840); *D. (D.) ricinus ricinus* (Linnaeus, 1758); *D. (D.) ricinus hadari* Emerson and Cernohorsky, new subspecies; *D. (D.) elegans* (Broderip and Sowerby, 1829); *D. (Ricinella) rubusidaeus* Röding, 1798; *D. (R.) speciosa* (Dunker, 1867); *D. (R.) clathrata clathrata* (Lamarck, 1816); *D. (R.) clathrata miticula* (Lamarck, 1822); *D. (Drupina) grossularia* Röding, 1798; and *D. (Drupina) lobata* (Blainville, 1832). Generic and specific synonymies are given for these taxa, together with distributional and ecological data for each species.

Indo-Pacific *Drupa*

Species of the genus *Drupa* Röding are confined in their distribution to the tropical Indo-Pacific region, where they are commonly encountered on intertidal reef-flats. *Drupa* species are muricacean gastropods which show a close relationship with the larger, but otherwise similar and closely related species of *Thais* Röding, and are currently assigned to the subfamily Thaidinae within the family Muricidae. Because of the close similarity in shell morphology, species of *Drupa* Röding, and *Morula* Schumacher have frequently been considered to be congeneric or only subgenerically separable. Wu (1965b), in his comparative study of the functional anatomy of the

digestive systems of *Drupa ricinus* (Linnaeus) and *Morula granulata* (Duclos), found morphological differences in features of the radula, gland-gut complex, stomach and rectal gland, and most notably in the structure of the salivary glands.

The exterior of the animal of *Drupa* consists of a foot with an attached, chitinous operculum, a head, snout, proboscis, a pair of tentacles and eyes and the reproductive organ. Animals are dioecious, with the male's penis situated behind the right tentacle below the thin mantle. The operculum is brown in color and corneous, stereotyped thaidine in appear-

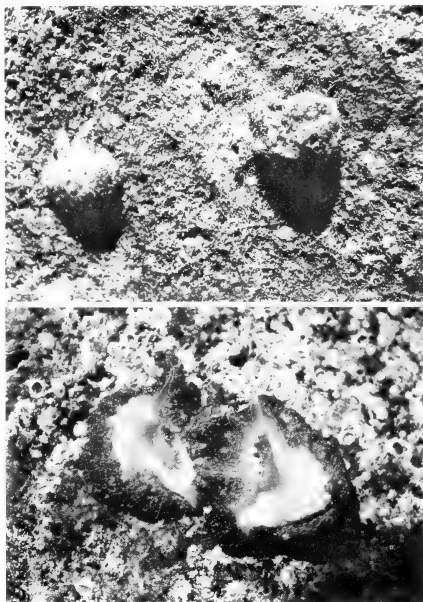


Plate 1. Camouflage in *Drupa (Drupina) grossularia* Röding. Cape Tuiolemu, Upolu, Samoa Ids. Top figure: Two specimens *in situ* on an exposed algae-covered reef. Bottom figure: two over-turned, living specimens on reef (photo courtesy A. Solem).

ance, with a series of plateaulike ridges on the side of attachment and concentric growth-rings on the exterior which converge basally into an ill-defined nucleus (see pl. 3, figs. 1-4).

In the Fiji Islands and the New Hebrides, *Drupa* were encountered in the mid-eulittoral and upper eulittoral region of the intertidal zone, generally on windward and exposed reef-flats. Species were considerably less numerous on protected, coral-strewn or shingle-covered leeward reefs. *Drupa morum* Röding, *D. rubusidaeus* Röding, and *D. ricinus* (Linnaeus) were most frequently collected on exposed algal ridges which were constantly kept moist through agitated waters and a breaking surf. The same species occurred on reef-edges covered with calcareous algae and detritus. *Drupa ricinus*, however, also occurred in the mid-eulittoral zone, while *D. grossularia* Röding, was usually confined to this part of the reef-zone. Kay (1971), in her study of the molluscan fauna of Fanning Island in the Line Islands, reported *D. ricinus*, *D. morum* and *D. grossularia* to be the most common macro-mollusks inhabiting reef-flats. *D. ricinus* and *D. grossularia* were among the dominant species of the beach-rock assemblages, with the former species restricted to exposed areas. *D. ricinus* also occurred on a subtidal, lagoonal patch reef, but was found to be far more abundant on seaward reefs than on the patch reefs in the lagoon. Salvat (1970), in his study of littoral molluscs of Fangataufa, Tuamotus, found a similar distributional pattern of *Drupa* as that observed by the junior author in Melanesia, with *D. ricinus* being more frequent on seaward algal ridges and *D. morum*

occupying the mid-eulittoral zone. Demond (1957) reported *D. grossularia* as occurring in Micronesia most commonly on windward reef flats on rocks near the low tide line, less frequently on leeward reefs and rarely in lagoons. *D. morum morum* was recorded commonly found living among rocks and coral of windward reef-flats and on windward lagoonal reef-flats of the larger atolls, but rarely on leeward reefs. This species was encountered most often near the low tide line, on or near the reef-edge, but also was taken in tide pools across the entire reef-flat. *D. ricinus* was reported to occupy a similar habitat to *D. morum morum*, while *D. rubusidaeus* was found to inhabit both windward and leeward reef-flats, living under rocks and coral rubble; it also occurred in tide-pools near, or just below the low tide line, and was found also living on coral heads off the seaward reef-edge, in 10 to 15 feet of water. Heinicke (1970) encountered *D. lobata* (Blainville), seemingly always occurring in pairs, in the lagoonal channel among coral heads at Diani Beach, Kenya.

Drupa species are commonly encrusted with algae, coral growth, vermetids, Foraminifera, *Hipponix* and other extraneous organisms, making them blend in with the substrate upon which they rest (see pl. 1). Nothing is known about natural enemies of *Drupa*, except that Schoenberg (1971) records captive *Conus textile* Linnaeus preying on *Drupa morum*, "*D. speciosa*" (= *D. rubusidaeus*), and both color forms of *D. ricinus*, among numerous other species of Hawaiian prosobranch gastropods.

Conflicting reports may be found in literature on the feeding habits of *Drupa* species. Salvat (1970) examined the microscopic con-

Figs. 1-3. *Drupa (Drupa) morum morum* Röding, 1798. 1, Chisimaio, Somalia (ANSP 298192); 2, 3, adult and immature, both from Okinawa Id. (ANSP 302877).

Figs. 4, 5. *Drupa (Drupa) morum iodosoma* (Lesson, 1840). Both from Ua Huka Id., Marquesas Ids. (ANSP 155617 and 156169).

Figs. 6-8, 11. *Drupa (Drupa) ricinus ricinus* (Linnaeus, 1758). 6, Okinawa Id. (ANSP 302919); 7, 11, Mahé, Seychelles Ids. (ANSP 266229); 8, immature, Moorea, Society Ids. (ANSP 283222).

Figs. 9, 10. *Drupa (Drupa) ricinus new subspecies hadari* Emerson and Cernohorsky. 9, paratype (AMNH 112617a); 10, holotype (AMNH 166928). Eilat, Gulf of Aqaba, Israel.

Figs. 12. *Drupa (Drupa) elegans* (Broderip and Sowerby, 1829). Society Islands (ANSP 199558).

Figs. 13-15. *Drupa (Ricinella) rubusidaeus* Röding, 1798. 13, Gesira, Somalia (ANSP 299187); 14, Isles Radama, N.W. Madagascar (ANSP 257243); 15, immature; Malaïta Id., British Solomon Ids. (ANSP 289624).

Figs. 16-18. *Drupa (Ricinella) clathrata clathrata* (Lamarck, 1816). 16, Okinawa Id. (ANSP 298725); 17, Hivaoa Id., Marquesa Ids. (ANSP 155492); 18, Pacific Ocean (ANSP 36720).

Figs. 19, 20. *Drupa (Ricinella) clathrata mitecula* (Lamarck, 1822). 19, Arsenal Bay, Mauritius (ANSP 273087); 20, Mahébourg, Mauritius (AMNH 104995).

Figs. 21, 22. *Drupa (Ricinella) speciosa* (Dunker, 1867). Both from "Rarotonga, Cook Ids."—probably an error (ANSP 29873). Known from the Tuamotus and Pitcairn Islands.

Figs. 23, 24. *Drupa (Drupina) grossularia* Röding, 1798. 23, Okinawa Id. (ANSP 225428); 24, immature, Sorsogon, Luzon Id., Philippines (ANSP 224148).

Figs. 25, 26. *Drupa (Drupina) lobata* (Blainville, 1832). 25, Mogadiscio, Somalia (ANSP 295772); 26, Direction Id., Cocos-Keeling Ids., Indian Ocean (ANSP 288455). (all figures about natural size)

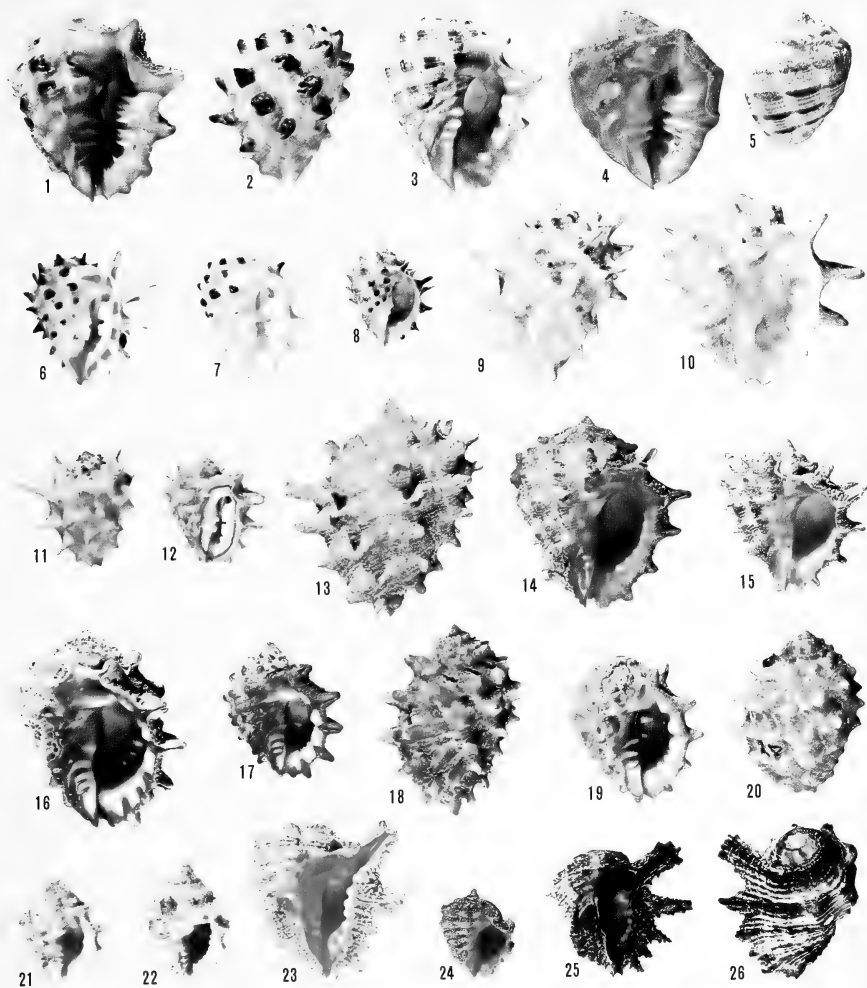


Plate 2. Genus *Drupa* Röding in the Indo-Pacific
(all figures about natural size)

Explanation on opposite page.

tents of the digestive tracts of several reef-dwelling gastropods and decided that *D. ricinus* and *D. morum morum* were herbivores, whereas other authors (Wu 1965b; Taylor 1968; Kay 1971; Cernohorsky, personal observation) report these species to be carnivores. The feeding habits of the following species have been reported:

Drupa morum morum

worms and sipunculids (Kay, 1971) [Line Ids.]

barnacle *Tetracita squamosa* (Taylor, 1968) [Seychelles Ids.]

herbivorous (Salvat, 1970) [Tuamotu Ids.]

sipunculid worms (Cernohorsky, pers. observation) [New Hebrides]

Drupa ricinus

live prey, i.e. sponges and holothurians, or carrion (Wu, 1965b) [Hawaiian Ids.]

molluscs, barnacles and worms (Kay 1971) [Line Ids.]

Drupa grossularia

omnivorous (Salvat, 1970) [Tuamotu Ids.]

In comparison to *Drupa* species, *Morula granulata* (Duclos) was reported to feed on other mollusks and barnacles in the Seychelles Islands (Taylor, 1968), but was recorded preying on holothurians, boring into bivalves of *Isognomon* and *Ostrea*, and consuming carrion in the Hawaiian Islands (Wu, 1965b).

No information is recorded on the mode of reproduction of *Drupa*, although J. B. Taylor (*in litt.*) reports certain Hawaiian species of *Drupa (sensu lato)* to have planktonic veligers. Such a larval stage would account for the wide distribution of most species.

Radulae

The radula of *Drupa* is of the rachiglossate type, with 3 teeth per transverse row with a formula of 1-1-1. The radular ribbon is small and very narrow, and the lateral teeth are simple and sickle-shaped (see pl. 4, fig. B). The rachidian teeth are more or less subquadrate or rectangular, the base is weakly concave, the central cusp is slender and longer than the flanking, bifid to quadrifid side-cusps. The lateral denticles are small, moderately deeply rooted and number from 2 to 5, and the end-cusps are usually slightly larger than the lateral denticles (see pl. 4, fig. A).

Although the shells of *Drupa* show an affinity with species of *Morula* Schumacher, the radulae of the muruline group of species differ in the following particulars: the central cusp of the rachidian is more deeply rooted, the flanking side-cusps are not multifid as in *Drupa*, but are simple, and the central cusp and side-cusps are separated from each other by an interposing small, intermediate cusp. The radula of *Morula* is essentially muricine in appearance while that of *Drupa* is a weakly modified thaidine radula, which approaches that of *Murex* s. s.

A classification based on radular morphology is complicated by the sporadic appearance of a drupine-type radula in other thaidine genera, e.g. *Agnewia tritoniformis* (Blainville, 1832) [see Kesteven, 1902, pl. 29, fig. 5 and Cooke, 1919, text fig. 26], *Semiricinula muricina* (Blainville, 1832) [see Arakawa, 1965, pl. 14, figs. 19, 20], and *Neothais smithi* (Brazier, 1889). Wu (1965b) surmized that the distinctive drupine and muruline radula pattern displayed by the species investigated by him may be directly associated with their respective feeding habits.

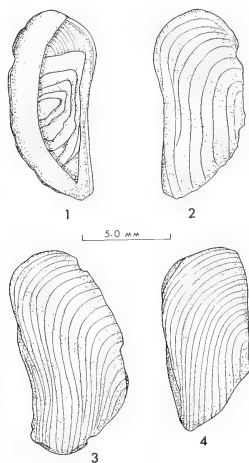


Plate 3. Opercula of *Drupa*.

Figs. 1, 2. *Drupa (Drupa) morum morum* Röding, from Nananu-i-Ra Id., Fiji Ids. 1, inner surface; 2, outer surface.

Fig. 3. *Drupa (Ricinella) clathrata clathrata* (Lamarck), from Pango Point, Efate Id., New Hebrides.

Fig. 4. *Drupa (Drupina) grossularia* Röding, from Wadigi Id., Fiji Ids.

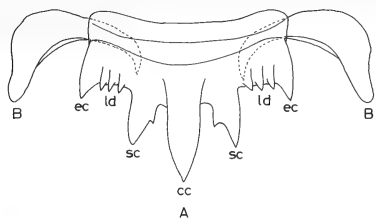


Plate 4. Radula of *Drupa (Drupa) ricinus ricinus* (Linnaeus).

One transverse row. Fig. A. rachidian or central tooth.

Fig. B. lateral tooth.

Abbreviations—

ec, end cusps

sc, side cusps

ld, lateral denticles

cc, central cusp

Distribution and fossil record

Species of *Drupa* are largely confined in distribution to the Indo-Pacific region, but some range from the northern regions of the Red Sea to Easter, Clipperton and the Galápagos Islands in the eastern Pacific Ocean. They inhabit tropical waters and do not occur beyond latitudes of 35°N and 35°S. Although muricacean gastropods date from the late Mesozoic in the Cretaceous, typical thaid gastropods first appear in the Oligocene in mid-Tertiary (Keen, 1971). These Cenozoic forms apparently are the precursors of the drupine forms that are here referred to *Drupa s.l.* The drupine forms, with low-spined, thaidlike shells having strong labial and columellar teeth, are poorly represented in the fossil record and are known only from the Pleistocene. Fossil moruline forms, with smaller, oval-biconical and higher-spined shells than those of *Drupa s.l.*, are recorded as ranging from the Eocene to the Pleistocene (Eames, 1971, as "*Drupa (Sistrum)*"). The limited paleontological data suggest, therefore, that *Drupa s.l.* and *Morula s.l.* evolved independently from a pre-thaid stock. The fossil evidence is not sufficient, however, to establish a well-documented evolutionary chronology of these generic groups.

As pointed out by Hertlein (1960), Paleogene fossils from Europe and the East Indies have been placed in the genera "*Ricinus*" or "*Sistrum*." A survey of the literature indicates that some of these taxa are not closely allied to *Drupa* or *Morula*. Cossmann (1889, p. 132; 1903, p. 80, pl. 3, fig. 15) refers *Purpura*

ringens Deshayes, 1865, from the Eocene of the Paris Basin to *Ricinus*, a spurious drupine assignment. Another example is *Sistrum baylei* Cossmann & Lambert, (1884, p. 175, pl. 5, fig. 19), from the Oligocene of France; both of these taxa appear to be buccinacean gastropods. *Purpura styriaca* Stur in Hilber, 1879, a Neogene fossil from the Miocene of Hungary, is a thaid, although this taxon was recently referred to *Drupa* by Strausz (1966, p. 284, fig. 130).

Ricinus puruensis Martin (1914, p. 147, pl. 4, fig. 104) [not fig. 105], described from the late Eocene of Java, appears to be the earliest record for the genus *Morula*. Miocene species of *Morula s.l.* include: *M. angasanana* (Martin, 1921, p. 466, pl. 59, fig. 52), *M. turrita* (Martin, 1880, p. 41, pl. 8, fig. 3), both from Java, *M. austriaca* (Hoernes & Auinger, 1882, pl. 16, figs. 14-17) from the Vienna Basin, and *M. inconstans* (Michelotti, 1847, p. 217) from Italy. Neogene fossils that are purported to represent living species of *Morula s.l.* are reported from Mio-Pliocene, Pliocene and Pleistocene deposits in the present Indo-Pacific faunal region and elsewhere.

Drupa s.str. is recorded by Eames (1971) as ranging from the Pliocene to Recent and as occurring in the Red Sea, Indo-Pacific, East Africa and questionably in North America. The New World record is based on the genus *Condonia* Hertlein, 1965, (type-species by original designation *Sistrum hannai* Howe, 1922), from the Pliocene of Oregon and California. This species, however, bears a resemblance to certain buccinacean shells, such as *Cantharus* and *Columbella*, and the monotypic genus *Condonia*, therefore appears to be referable to the superfamily Buccinacea instead of the Muriceae.

Pentadactylus rhombiformis Martin (1899, p. 138, pl. 21, figs. 316a, b), described from the Pliocene of Java, was compared with several living muricacean species, including references to Reeve's (1846, *Purpura*, pl. 3, fig. 13) illustration of *Drupa rubusidaeus* Röding. The species was considered closest in relationship to *Purpura muricina* Blainville, and the description and illustration of the Indonesian fossil suggest that it is a spinose thaid.

Thus the available data indicate no valid records for *Drupa s.l.* prior to the Pleistocene. The following species are reported from Pleistocene deposits: *Drupa (Drupa) morum* Röding, 1798; *D. (D.) ricinus ricinus* (Linnaeus,

1758), and *Drupa* (*Ricinella*) *rubusidaeus* Röding, 1798 (see distributional records).

Classification

The Linnaean species of *Drupa* s.l. were originally described in the genus *Murex* Linnaeus. Röding (1798) proposed the genus *Drupa*; Montfort (1810) the genus *Sistrum*; and Lamarck (1816) the genus *Ricinula*, all for some of the drupine species previously assigned to *Murex*. The genus-group name *Ricinula* remained in use in malacological literature until about 1913, when it was gradually replaced with Röding's chronologically prior *Drupa*.

Thiele (1929) accepted *Drupa* as a valid genus-group, but relegated several moruline genera, i.e. *Cronia* H. & A. Adams, *Morulina* Dall (= *Azumamorula* Emerson), *Phrygiomurex* Dall, *Maculotriton* Dall and *Drupella* Thiele, as subgenera of *Drupa*. Wenz (1941) erected the new subfamily Drupinae, which besides the type-genus *Drupa*, contained the genus *Thais* Röding and other thaid genera, together with the non-thaid genus *Tritonalia* Fleming (= *Ocenebra* Gray). Drupinae Wenz, 1938 and 1941 is presently considered a junior synonym of Thaidinae Suter, 1909 (as Thaisidae Suter, 1909, Rec. Canterbury Mus., vol. 1, p. 11; 1909, Subantarctic Islands of New Zealand, art. 1, p. 27). The subfamilial name Thaidinae was conserved by action of the International Commission on Zoological Nomenclature (Opinion 886, 1969) in preference to the chronologically older, but less frequently used Purpurinae.

Species of *Drupa* are here assigned to the genus mainly on shell-morphology, although radular characters have also been considered. As pointed out in the section on "Radulae," a classification on radular characters alone would require an inclusion of species of *Agnewia*, *Semiricinula*, *Neothais* and a species of *Morula*. Such a classification was in fact proposed by Cooke (1919), who included 7 non-drupine species in *Drupa* on the basis of radular characters which he considered "distinctly of the *Drupa* type." It is obvious that on shell-morphology alone, the limits of *Drupa* are well-defined, but radular characters of *Drupa* also appear rarely in species referable to other thaidine genera.

Due to the dispersal at auction of the Bolten collection, on whose specimens Röding's new

descriptions were based, the whereabouts of the type-specimens are no longer known. F. C. Schmidt did purchase a small part of Bolten's collection in 1819, but in a letter written by him, he observed that a great amount of the collection was purchased by Hamburg buyers. From those specimens procured by Schmidt from the Bolten collection, now in the Naturkundemuseum, Staatliche Museen zu Gotha, Germany, only very few can be traced back to Bolten (Dr. Motschmann, *in litt.*). In the absence of Röding's type-specimens we have designated appropriate cited illustrations of specimens figured by other authors as lecto-types of Röding's species.

List of Recognized Taxa

Below are listed the recognized generic and specific taxa for the genus *Drupa*. The eleven species and subspecies are referred to three genus-groups. All are living, and three are also recorded as Pleistocene fossils.

Family Muricidae Rafinesque, 1815

Subfamily Thaidinae Suter, 1909

GENUS *Drupa* Röding, 1798

Subgenus *Drupa* Röding, 1798

morum morum Röding, 1798. **Type** species.

Recent. Indo-Pacific. and Eastern Pacific, except the Marquesas Islands. Pleistocene.

morum iodostoma (Lesson, 1840). Recent, Marquesas Islands.

ricinus ricinus (Linnaeus, 1758). Recent, Indo-Pacific and Eastern Pacific. Pleistocene.

ricinus hadari Emerson and Cernohorsky, new subspecies. Recent, Red Sea.

elegans (Broderip and Sowerby, 1829). Recent, Wake Island to the Tuamotu Islands.

Subgenus *Ricinella* Schumacher, 1817

rubusidaeus Röding, 1798. **Type** species. Recent, Indo-Pacific. Pleistocene.

speciosa (Dunker, 1867). Recent, Tuamotu and Pitcairn Islands.

clathrata clathrata (Lamarck, 1816). Recent, tropical west Pacific Ocean.

clathrata miticula (Lamarck, 1822). Recent, Indian Ocean.

Subgenus *Drupina* Dall, 1923

grossularia Röding, 1798. **Type** species. Recent, East Indian Ocean and Pacific.

lobata (Blainville, 1832). Recent, Indian Ocean.

Abbreviations

The following institutional abbreviations are used in this paper:

AIM—Auckland Institute and Museum, Auckland

AMNH—American Museum of Natural History, New York

AMS—Australian Museum, Sydney

ANSP—Academy of Natural Sciences of Philadelphia

BM (NH)—British Museum (Natural History), London

BPBM—Bernice P. Bishop Museum, Honolulu

DM—Dominion Museum, Wellington

DMNH—Delaware Museum of Natural History, Greenville

FMNH—Field Museum of Natural History, Chicago

MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts

LACMNH—Los Angeles County Museum of Natural History

MHNG—Museum d'Histoire Naturelle, Geneva

SDMNH—San Diego Museum of Natural History

USNM—National Museum of Natural History, Washington, D.C.

WAM—Western Australian Museum, Perth

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Species excluded from *Drupa*

Included under this heading are species of Thaidinae which were originally described in *Drupa*, or have been referred to this genus by subsequent authors. In the latter category, only those species requiring further explanation have been listed.

Neothais bollonsi (Suter, 1906)

(Pls. 5, 6)

Remarks—Suter (1909) assigned this moruline species to the genus *Drupa* on the basis of the typically drupine radula. Iredale (1915) correctly synonymized *D. bollonsi* with the southeast Australian species *Purpura smithi* Brazier, 1889, and assigned it to the genus *Neothais* Iredale, 1912. Despite its drupine radular characters, the species should be placed near *Morula* Schumacher.

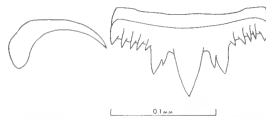


Plate 5. Radula of *Neothais smithi* (Brazier). Half a transverse row; Sunday Id., Kermadec Ids. [synonym is *Drupa bollonsi* Suter].

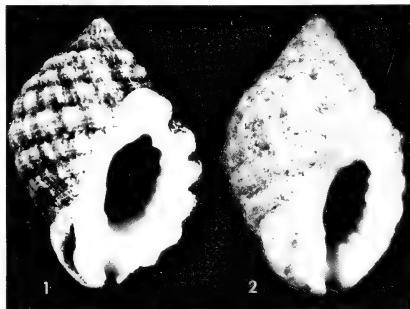


Plate 6. *Neothais smithi* (Brazier). [synonym is *Drupa bollonsi* Suter].

Fig. 1. Sunday Id., Kermadec Ids. (AIM; 24.5 x 17.4 mm).

Fig. 2. Norfolk Id. (AIM; 18.0 x 12.0 mm).

Synonymy—

- 1889 *Purpura smithi* Brazier, Australian Museum Memoir, no. 2, p. 28, pl. 4, figs. 1-4, 7-12, 21-22 (Lord Howe Id.) [as *Purpura (Polytropia) smithi* on plate explanation].
- 1902 *Purpura tritoniformis* var. *smithi* Brazier, Kesteven, Proceedings of the Linnaean Society of New South Wales, pt. 4, p. 534.
- 1906 *Purpura striata* Martyn subsp. *bollonsi* Suter, Transactions and Proceedings New Zealand Institute, vol. 38, p. 331 (Kermadec Ids.).
- 1909 *Drupa bollonsi* Suter, Proceedings of the Malacological Society of London, vol. 8, p. 254, pl. 11, figs. 5-7 (shell, operculum and radula); 1913 Suter, Manual of the New Zealand Mollusca, p. 428, pl. 19, fig. 11 (New Zealand).
- 1915 *Neothais smithi* (Brazier), Iredale, Transactions and Proceedings New Zealand Institute, vol. 47, pp. 474, 475; 1915 Oliver, Transactions and Proceedings New Zealand Institute, vol. 47, p. 536; 1950 Dell, Dominion Museum Records, Zoology, vol. 1, no. 3, p. 26.

Condonia hannai (Howe, 1922)

Remarks—This moderately large, (66.8 mm long) species from the Pliocene of Oregon and California was originally described in the genus *Sistrum* Montfort. Hertlein (1965) proposed for this species the new genus *Condonia*, and placed the genus in the muricid subfamily "Drupinae" with apparent reluctance. He concluded that: "*Condonia hannai* bears a general resemblance to the Recent *Drupa iodostoma* Lesson . . . but the spire of that species is low and the columella [=error for inner margin of outer lip] bears denticles typical of *Drupa*." He also noted that the genus was not known as a fossil in the Eastern Pacific region, but that living representatives occur in the Galápagos Islands and at Clipperton Island. Although the labial dentition does superficially resemble that of *Drupa*, the type-species of *Condonia* lacks columellar denticles. This extinct species appears to be a buccinacean gastropod, and Dr. G. E. Radwin (in litt.) considers *Condonia hannai* to be an extralimital representative of the genus *Columbella* s.str. which, perhaps due to its unusual northern, cooler-water habitat, attained a giant size. The monotypic genus *Condonia*, therefore, appears to be referable to the Buccinacea rather than the Muricacea.

Synonymy—

- 1922 *Sistrum hannai* Howe, Univ. California Publ., Bull. Dept. Geol. Sci., vol. 14, no. 3, p. 102, pl. 8, figs. 1, 5 (Fossil Point, S. W. Empire City, Coos Bay, Pliocene of Oregon); 1943 Weaver, Univ. Washington Publ. Geology, vol. 5, pt. 2, p. 450, pl. 87, figs. 14,

16 (figured holotype); 1960 Hertlein, Veliger, vol. 3, no. 1, p. 8 (San Benito County, Pliocene of California).

- 1965 *Condonia hannai* (Howe), Hertlein, Occas. Papers California Acad. Sciences no. 49, p. 4, figs. 3, 4 (figured holotype).

Azumamorula mutica (Lamarck, 1816)

(Pls. 7, 8)

Remarks—For the western Indian Ocean species *Ricinula mutica* Lamarck, which is intermediate in shell-characters between *Drupa* Röding, and *Morula* Schumacher, Dall (1923) proposed the genus-group *Morulina*. Thiele (1929) and Wenz (1941) assigned *Morulina* as a subgenus to *Drupa*. Emerson (1968) proposed the substitute name *Azumamorula* for the preoccupied *Morulina* Dall (non *Morulina* Börner, 1906, in Insecta), and figured the radula of the type-species, which is typically moruline.



Plate 7. Radula of *Azumamorula mutica* (Lamarck). Half a transverse row; Black River Bay, Mauritius (after Azuma and d'Attilio in Emerson, 1968).

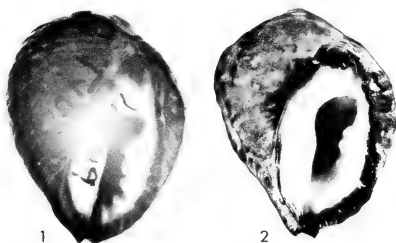


Plate 8. *Azumamorula mutica* (Lamarck).

Fig. 1. Holotype from unknown locality ("Mozambique" on label) [MHNG no. 1101/19; 20.2 x 16.5 mm].

Synonymy—

- 1816 *Ricinula mutica* Lamarck, Tabl. Encycl. Méthodique, p. 1, pl. 395, figs. 2a, b (no locality given); 1846 Reeve, Conchologia Iconica, vol. 3, pl. 2, fig. 1.
- 1822 *Ricinula pisolina* Lamarck, Hist. nat. anim. s. vertèbres, vol. 7, p. 233 (Ile de France - Mauritius); 1835 Kiener, Spéc. gén. icon. coquilles vivantes, vol. 8, p. 20, pl. 4, fig. 8a (juvenile specimen); 1844 Deshayes and Milne-Edwards, Hist. Nat. anim. s. vertèbres, ed. 2, vol. 10, p. 52.
- 1919 *Morula mutica* (Lamarck), Cooke, Proceedings of the Malacological Society of London, vol. 13, p. 106 (description of radula).

- 1923 *Morulina mutica* Lamarck, Dall, Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 75, p. 303.
- 1929 *Drupa (Morulina) mutica* (Lamarck), Thiele, Handb. syst. Weichtierkunde, vol. 1, p. 294; 1941 Wenz, Handb. Paläozoologie, vol. 6, pt. 5, p. 1112, text fig. 3159.
- 1968 *Azumamorula mutica* (Lamarck), Emerson, Nautilus, vol. 81, no. 4, p. 125, text fig. (radula).

***Drupa vitiensis* Pilsbry in
Pilsbry and Bryan, 1918**

Remarks—The species illustrated by Pilsbry and Bryan is the male form of *Drupella cornus* (Röding, 1798). Generally credited to Pilsbry, 1921, the specific name was validated by Pilsbry and Bryan through a published illustration in combination with a specific name.

Synonymy—

- 1918 *Drupa vitiensis* Pilsbry in Pilsbry & Bryan, Nautilus, vol. 31, no. 3, pl. 9, fig. 5.
- 1921 *Sistrum vitiense* Pilsbry, Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 72, p. 319 (Fiji Ids.).

***Drupa walkerae* Pilsbry and Bryan, 1918**

Remarks—The species described by the authors belongs to *Drupella* Thiele, 1925, and is similar to, if not conspecific with *D. rugosa* (Born, 1778).

Synonymy—

- 1918 *Drupa walkerae* Pilsbry & Bryan, Nautilus, vol. 31, no. 3, p. 99, pl. 9, fig. 4 (Honolulu Harbor, Hawaiian Ids.).

Röding (1798) described in the *Museum Boletianum*, pp. 55-56, the following *Drupa* species: *D. chamaemorus*, *D. botroides*, *D. uva*, *D. cornus*, *D. glans*, *D. muricina*, *D. mancinella*, *D. trapa* and *D. aesculus*. All these taxa are non-drupine species referable to various thaidine genera, with the exception of *D. glans*, which belongs to the genus *Austrofusus* Kobelt, 1879, in the family Buccinidae.

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Family Muricidae Rafinesque, 1815

Subfamily Thaidinae Suter, 1909

Key To Subgeneric Groups of Indo-Pacific Drupa

- A. Columella singularly folded axially B
- B. Labial teeth compound,
 constricting the aperture *Drupa s.str.* p. 14-819
- BB. Labial teeth singularly arranged or
 occasionally in close association, not compound,
 aperture not constricted *Ricinella* p. 14-841
- AA. Columella doubly folded axially; margin of outer lip
 with 2 digitate processes, aperture narrow,
 not constricted *Drupina* p. 14-859

Subfamily Thaidinae Suter, 1909

The subfamily name Thaidinae has been granted precedence over the long established family-group name Purpuridae Menke, 1828, in Opinion 886 of the International Commission on Zoological Nomenclature. Although the Commission has dated Thaidinae Suter from 1913, Suter erected the family-group name in 2 prior publications in 1909 (see synonymy).

Authors generally divide the family Muricidae into 7 subfamilies: the Muricinae, Ocenebrinae, Aspellinae, Thaidinae, Trophoninae, Typhinae and Rapaninae. Some authors, however, consider the Thaidinae worthy of family rank, but since no scientific evidence as to important anatomical, morphological or ecological differences between the Thaidinae and other closely related muricid groups has been presented, an elevation of Thaidinae to family rank appears unwarranted. In such a closely related species-group as the Muricidae, with numerous existing species of intermediate generic characters, a taxonomic consolidation rather than further subdivision, is indicated.

Apart from the nominate type-genus *Thais* Röding, 1798, the subfamily Thaidinae contains such genera as *Mancinella* Link, 1807, *Acanthina* Fischer von Waldheim, 1807, *Cymia* Mörch, 1860, *Purpura* Bruguière, 1789, *Nucella* Röding, 1798, *Nassa* Röding, 1798, *Vexilla* Swainson, 1840, *Pinaxia* H. & A. Adams, 1853, *Xanthochorus* Fischer, 1888, *Morula* Schumacher, 1817, *Azumamorula* Emerson, 1968, *Drupella* Thiele, 1925, *Neothais* Iredale, 1912, *Lepsiella* Iredale, 1912, *Agnewia* Tenison-Woods, 1878, *Cronia* H. & A. Adams, 1853, and other subgeneric groups and fossil genera.

Synonymy—

- 1828 Purpuracea Menke, Synopsis methodica Molluscorum, p. 34 (suppressed by the ICZN in Opinion 886, 1969, Bull. zool. Nomenclature, vol. 26, pp. 128-132).
- 1839 Purpuridae Broderip, Penny Cyclop., vol. 14, p. 321 (suppressed in Opinion 886 of ICZN).
- 1840 Purpurinae Swainson, Treatise on Malacology, p. 71 (suppressed in Opinion 886 of ICZN).
- 1909 Thaisidae Suter, Records Canterbury Museum, vol. 1, p. 11; 1909 Suter, Subantarctic Islands of New Zealand, art. 1, p. 27.
- 1938 Drupinae Wenz, Handbuch der Paläozoologie, vol. 6, pt. 1, pp. 42, 47; 1941 Wenz, *ibid.*, pt. 3, p. 1112.

Subfamily Thaidinae Suter, 1909

Genus *Drupa* Röding, 1798

Type: *Drupa morum* Röding, 1798

On shell characters, the group generally considered as belonging to *Drupa* s.str. can be divided into two distinct groups. In the group of the type-species *Drupa morum* Röding, which also includes the subspecies *D. morum iodostoma* (Lesson), *D. ricinus* (Linnaeus) and *D. elegans* (Broderip & Sowerby), the majority of the denticles on the outer lip are arranged as compound, i.e. bifid or trifid teeth which constrict the aperture posteriorly. In the group comprising *D. rubusidaeus* Röding, *D. speciosa* (Dunker) and *D. clathrata* (Lamarck), the denticles of the outer lip are singularly situated as non-compound teeth, which results in an appreciably wider aperture. For this group of species the subgeneric name *Ricinella* Schumacher, 1817, is available. Although the teeth on the outer lip of *Drupa* (*Drupina*) *grossularia* Röding, the type-species of the subgenus *Drupina* Dall, are also singularly arranged, the shell of the species develops marginal lobate processes and the radula has a greatly modified rachidian radular tooth and very slender and small lateral teeth.

Drupa differs from *Morula* in having a more sub-ovate form, lower spire, longer aperture and a structurally different central radular tooth. Members of *Drupa* show a close radular relationship with most of the thaidine groups.

Synonymy—

- 1798 *Drupa* Röding, Museum Boltenianum, p. 55. Type-species by subsequent designation, Rovereto, 1899: *Drupa morum* Röding, 1798.
- 1807 *Canrena* Link, Besch. Nat.-Samml. Univ. Rostock, p. 126. Type-species by monotypy: *Canrena neritoides* Link, 1807 [= *Drupa morum* Röding, 1798] (as restricted by Iredale, 1937, and lectotype designation by Cernohorsky, 1969).
- 1810 *Sistrum* Montfort, Conchyliologie systématique, vol. 2, p. 595. Type-species by original designation: *Sistrum album* Montfort, 1810 [= *Drupa ricinus* (Linnaeus, 1758)].
- 1816 *Ricinula* Lamarck, Tableau Encyclopédique et Méthodique, p. 1. Type-species by subsequent designation, Children, 1823: *Ricinula horrida* (= *R. horrida* Lamarck) [= *Drupa morum* Röding, 1798].
- 1822 "*Ricinella* Lam.", Bowdich, Elements of Conchology, vol. 1, p. 40. [? error for *Ricinula* Lamarck, 1816] (sole species listed and figured *Ricinula horrida* Lamarck, 1816) [non *Ricinella* Schumacher, 1816].
- 1852 *Pentadactylus* Mörch, Catal. Conchyl. Yoldi, vol. 1, p. 87. Type-species by subsequent designation, Baker, 1895: *Pentadactylus ricinus* Lamarck = *Drupa ricinus* (Linnaeus, 1758). [non *Pentadactylus* Schultze, 1760, in Echinodermata; nec Gray, 1845, in Reptilia].
- 1855 *Ricinula* Gould, U.S. Astronom. Exp. South. Hemisphere, vol. 2, p. 263 (error for *Ricinula* Lamarck, 1816).
- 1859 *Ricinulus* Demarest in Chenu, Encycl. Hist. Nat. Crust. Moll. Zooph., p. 174 (invalid emendation for *Ricinula* Lamarck, 1816).

As pointed out by the junior author (Cernohorsky, 1969), Suter (1913) is credited by Dodge (1957) and other authors with the type designation of *Drupa*, but Rovereto's (1899) designation is earlier.

Although members of this genus were placed until the turn of the present century in Lamarck's *Ricinula*, there were available

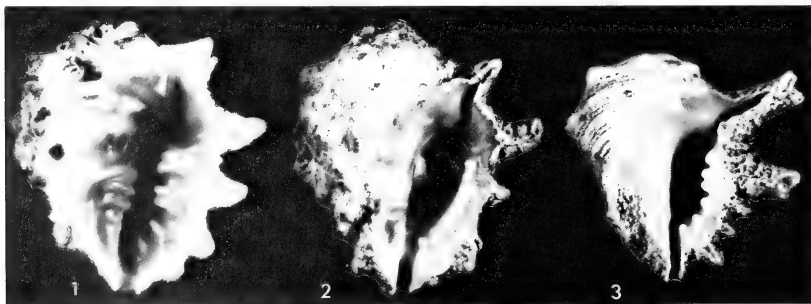


Plate 9. Type-species of subgenera of *Drupa* Röding.

Fig. 1. *Drupa* (*Drupa*) *morum* Röding. Namoui reef, Niue Id. (WOC coll.; 29.8 x 27.4 mm).

Fig. 2. *Drupa* (*Ricinella*) *rubusidaeus* Röding. Suva reef, Fiji Ids. (WOC coll.; 40.5 x 36.5 mm).

Fig. 3. *Drupa* (*Drupina*) *grossularia* Röding. Pango Point, Efate Id., New Hebrides (WOC coll.; 28.3 x 28.6 mm).

three valid prior generic names, of which *Drupa* Röding, 1798, is the oldest. Link, 1807, established *Canrena* as a monotypic genus with *Canrena neritoidea* Link, the sole species. His citation to Martini's figures include the species *Drupa ricinus* (Linnaeus), *D. morum* Röding, and *D. grossularia* Röding. *Canrena neritoidea* was restricted by Iredale (1937) to *Drupa morum* Röding, as depicted by Martini's figures 972, 973, on plate 101. The same figures were designated as the lectotype of the species *Canrena neritoidea* Link, by Cernohorsky (1969).

The monotypic genus *Sistrum* Montfort, 1810, has been erroneously used by many authors for the species rightly contained in *Morula* Schumacher, 1817, which has *Drupa uva* Röding, as the type-species. *Sistrum album* Montfort, the type-species of *Sistrum* by original designation, is a synonym of *Drupa ricinus* (Linnaeus). In his discussion of *Sistrum album*, Montfort considered the species to have a white, violet or yellowish aperture, a misconception common with writers of the day. Although the violet aperture would indicate the species *Drupa morum*, Montfort's figure of *Sistrum album*, the specific name itself and its French, Dutch and Flemish equivalents of "Le Sistre blanc," "La mure blanche," "wite moerbiesie" and "witte moerbeyer," all refer to the white-mouthed form of *Drupa ricinus* (Linnaeus).

Subgenus *Drupa sensu stricto*

Shell small to medium, strong, heavy, sub-ovate; whorls low or conical, often with siphonous tubercles, 2 tubercles rarely extended from the margin as lobate processes; surface generally sculptured with imbricated scales; aperture noticeably constricted posteriorly by labial teeth; teeth arranged in compound groups; columella typically with 1 prominent axial fold, rarely with 2 folds, and with 3-5 prominent oblique plications; radular formula 1-1-1, lateral teeth fang-like, similar in shape, central tooth typically composed of a large medial cusp, flanked by a pair of slightly smaller, bifid to quadridid cusps, and small, slender lateral denticles; operculum sub-lunar to sub-linear, nucleus marginal, marginal callus well developed, muscle scars few in number, arranged as gyrate lines.

Members of this genus are typical coral and reef forms, being confined to the tropical

waters of the Indo-Pacific region, although some species occur at Easter, Clipperton and the Galápagos Islands, in the tropical eastern Pacific.

Drupa morum morum Röding, 1798

(Pl. 2, figs. 1-3; Pls. 10, 11)

Range—Red Sea and East Africa to the Eastern Pacific including Easter and Clipperton Islands (except the Marquesas Islands).

Remarks—The purple-colored aperture and the shorter tubercles distinguish this species from the white- or yellow-mouthed form of *D. ricinus*. The possession of tubercles, the deeper purple color of the aperture and the lack of dorsal bands offset this from the Marquesan subspecies *D. morum iodostoma* (Lesson, 1840).

Habitat—Intertidal on reef-flats, among rocks and in crevices; frequently found near the reef-edge on reefs exposed to strong surf.

Description—Shell 18 to 49 mm ($\frac{3}{4}$ to 2 inches) in length, ovately globose, spire acuminate, generally inconspicuous in adult stage. Whorls nodose with four rows of short, strong tubercles. Interstices between tubercles striated with scalelike striae. Aperture narrow, linear, extending nearly three-quarter the length of the shell. Outer lip crenulated between tubercles, dentate on the interior margin with plaitlike teeth; teeth arranged in an upper group of four denticles and in a lower group of three denticles. Two conspicuous plaits situated immediately above the deep canal. Inner lip enameled with a callus containing 3 or 4 plaitlike ridges projecting into the aperture above the canal. Posterior siphonal canal elongate, obliquely recurved toward the apex. Color white or grayish, tubercles dark-brown; interior of aperture deep purple in adults, light purple in immature specimens. Operculum typical of the group.

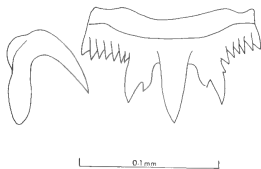


Plate 10. Radula of *Drupa (Drupa) morum morum* Röding. Half a transverse row; Fiji Ids.

The central cusp of the rachidian of the radula is slightly longer than the flanking and bifid side-cusps; the side-cusps are followed by 3 to 5 small lateral denticles, exclusive of the slightly stronger end-cusps. In some specimens, the lateral denticles descend onto the side-cusps.

Measurements (mm)—(including spines; all specimens with a mature lip).

length	width	
49.1	45.9	S. E. Zanzibar
40.0		Lectotype of <i>horrida</i> Lamarck
32.4	29.6	Tosa, Japan
27.0	23.7	Viti Levu, Fiji
18.1	17.1	Bikini Atoll, Marshalls

Synonymy—

- 1684 ——— Buonnanni, Rec. ment. oculi anim. test., (3), fig. 173 only (very poor).
 1685 ——— Lister, Hist. Syn. Meth. Conchyliorum, pl. 804, fig. 13.
 1753 ——— Klein, Tent. meth. ostr. nat. cochl., pl. 1, fig. 30.
 1758 *Nerita nodosa* Linnaeus (*pars*), Systema Naturae, ed. 10, p. 777 (refers to Lister, Klein and Buonnanni, (fig. 173) only).
 1767 *Murex neritoides* Linnaeus (*pars*), Systema Naturae, ed. 12, p. 1219 (refers to Lister, Klein and Buonnanni (fig. 173) only; 1791 Gmelin (*pars*), Systema Naturae, ed. 13, p. 3537 (refers to Lister (fig. 13) only, Buonnanni, Klein, Knorr and Martini (figs. 972, 973 only) and Seba (fig. 41 only); 1825 Wood, Index Testaceologicus, p. 123, pl. 26, fig. 47a).
 1768 ——— Knorr, Verg. Augen u. Gemüths, pt. 1, pl. 25, figs. 5, 6 (good).
 1777 "*Murex Morum globosum*" Martini, Syst. Conchylien-Cabinet, vol. 3, p. 280, pl. 101, figs. 972, 973 (East Indies and coast of Coromandel) [non binomial].
 1798 *Drupa morum* Röding, Museum Boltenianum, p. 55 (refers to Martini and Knorr) [no locality given]; 1913 Hedley, Nautilus, vol. 27, no. 7, p. 80; 1936 Hirase, Coll. Jap. shells, p. 79, pl. 110, fig. 8; 1957 Kaicher, Indo-Pacific Sea Shells, pl. 4, fig. 3; 1960 Hertlein, Veliger, vol. 3, no. 1, p. 8 (Galápagos and Clipperton Ids.); 1961 Rippingale & McMichael, Queensland and Gt. Barrier reef shells, pl. 13, fig. 5; 1965 Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 114, pl. 13, figs. 3, 4 (radula); 1965 Wu, Bull. Inst. Zool. Acad. Sinica, vol. 4, p. 98, text fig. 19 (radula); 1967 Orr Maes, Proc. Acad. Nat. Sci. Philadelphia, vol. 119, no. 4, p. 129; 1969 Cernohorsky, Veliger, vol. 11, no. 4, p. 298, pl. 47, fig. 7 (shell), text fig. 4 (radula); 1970 Salvat, Cahiers du Pacifique, no. 14, p. 46; 1971 Wilson & Gillett, Australian Shells, p. 92, pl. 61, fig. 2; 1971 Kay, Pacific Science, vol. 25, pp. 266, 275.
 1807 *Canrena neritoides* Link, Besch. Nat.-Samml. Univ. Rostock, 3 Abth., p. 126 (refers to Martini, pl. 101, figs. 972, 973—designated as lectotype figures by Cernohorsky, 1969) [no locality given].
 1816 *Ricinula horrida* Lamarck, Tabl. Encycl. Methodique, p. 1, pl. 395, figs. 1a, b (no locality given); 1822 Lamarck, Hist. nat. anim. s. vertèbres, vol. 7, p. 231 (Indian Ocean); 1823 Sowerby, Genera Rec. foss. shells, pt. 18, pl. 235, fig. 1; 1842 Reeve, Conchologia Systematica, vol. 2, p. 215, pl. 156, fig. 1; 1846 Reeve, Conchologia Iconica, vol. 3, pl. 1, fig. 3; 1859 Chenu, Manuel Conchyliologie,

- vol. 1, p. 168, fig. 814; 1880 Tryon, Manual Conchology, vol. 2, p. 184, pl. 56, figs. 201, 202; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 238.
 1817 *Ricinella violacea* Schumacher, Essai Nouv. Système, p. 240 (refers to Martini, *op. cit.*) [no locality given].
 1823 *Ricinula horrida* (sic) Children, Quart. Journ. Sci. Lit. & Arts, vol. 16, p. 56, pl. 5, fig. 189.
 1832 *Purpura horrida* Lamarck, Blainville, Nouv. Ann. Mus. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 208; 1833 Quoy & Gaimard, Voyage L'Astrolabe, vol. 2, p. 576, pl. 39, figs. 1-3 (animal and operculum); 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 8, pl. 1, fig. 1 (animal).
 1850 *Sistrum horridum* M. Gray, Figs. Moll. Animals, vol. 4, p. 70, pl. 96, fig. 11; 1911 Schepman, Siboga-Expeditie, vol. 49d, p. 355; 1952 Morris, Field Guide shells Pacific coast and Hawaii, pl. 39, fig. 5.
 1852 *Ricinula* (*Pentadactylus*) *globosa* Mart., Mörch, Cat. Conchyl. Yoldi, vol. 1, p. 88 (synonymized with *R. horrida* Lamarck and *Drupa morum* Röding).
 1853 *Pentadactylus* (*Pentadactylus*) *globosus* H. & A. Adams, Genera Rec. Mollusca, vol. 1, pp. 129, 130, pl. 13, fig. 6 (animal).
 1908 *Pentadactylus* (*Pentadactylus*) *horridus* Lamarck, Horst & Schepman, Cat. Syst. Moll. Mus. Hist. Nat. Pays-Bas, vol. 13, p. 157.
 1938 *Drupa* (*Drupa*) *morum* Röding, Adam & Leloup, Mém. Mus. Roy. d'Hist. Nat. Belg., vol. 2, fasc. 19, p. 164.

Types—Since Röding's types are probably no longer extant, we designate the specimen depicted on plate 101, figs. 972, 973 in Martini, as the lectotype of *Drupa morum* Röding (pl. 11 fig. 1). Two syntypes of *Ricinula horrida* Lamarck, are in the Muséum d'Histoire Naturelle, Geneva; the specimen measuring 40.0 mm in length, no. 1101/12/1, is here selected as the lectotype of *R. horrida*. The type-specimen of *Ricinella violacea* Schumacher, could not be located in the University Zoological Museum, Copenhagen. From the two localities mentioned by Martini for *D. morum* s. s. we select the first-mentioned "East Indies" as the

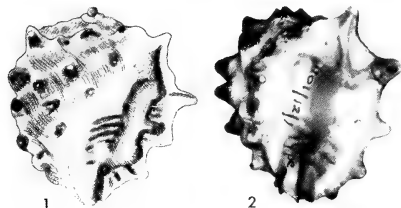


Plate 11. *Drupa* (*Drupa*) *morum morum* Röding.

Fig. 1. Lectotype figure from Martini, 1777, Syst. Conchylien-Cabinet, vol. 3, pl. 101, fig. 972.

Fig. 2. Lectotype of *Ricinula horrida* Lamarck (MHNG no. 1101/12/1; 40.0 x 38.2 mm).

type locality, and restrict it further to Java, Indonesia (specimens in AMNH and ANSP).

Nomenclature—This species was well known to early naturalists but was confused by Linnaeus with *Thais nodosa* and *T. nodosa ascensionis* Quoy & Gaimard (= *meretricula* Röding). In his 12th edition of the "Systema Naturae," Linnaeus re-named the species *Murex neritoideus*, and cited the same erroneous figures which depict *Drupa morum*. However, in Linnaeus' personal copy of the 12th edition of the "Systema Naturae," the complete synonymy of the 10th edition description of *Nerita nodosa* has been cancelled and the following words were added: "Labium interius punctis 2 maculatum."

Records—RED SEA: Lahonel Beach, Gulf of Aqaba, Israel (Lamy, 1938, p. 56); Berenice, Egypt (ANSP); Mahmud reef, Jiddah, Saudi Arabia (AMNH). EAST AFRICA: SE Point, Isla di Serpenti, Chisimaio, Somalia (AMNH); Pangavini Id., 10 mi. NNE Dar-es-Salaam, Tanzania (MCZ); Diani Beach, Kenya (Heinicke, 1970, p. 7); Mozambique (USNM). ZANZIBAR: Chumbe Id.; Kivengwa; Ras Nungwe (all ANSP). SEYCHELLES: (AMNH); Cousin Id. (ANSP). MADAGASCAR: S. side of Nossi Iranja, 32 mi. SW of Nossi Bé; Flacourt, Fort Dauphin; 2 mi. NE Point Ansirakiraky (all MCZ). MAURITIUS: 1 mi. ESE of Souillac; Pointe Fayette (both ANSP); near Port Louis (MCZ); Point Piment, N. side Arsenal Bay (Powell coll.). REUNION ISLAND: (ANSP). CHAGOS ARCHIPELAGO: (Melville, 1909, p. 104). MALDIVES ISLANDS: Imma Id., SE North Male Atoll; Fadiffolu Atoll; Tiladummati Atoll (all ANSP). LACCADIVE ISLANDS: (Hornell, 1922, p. 217). INDIA: Pamban and Shingle Id., Gulf of Manar (Satyapuri, 1952, p. 160). CEYLON: 12 mi. N. of Trincomalee (AMNH); Hikkaduwa (ANSP). THAILAND: Loam Seng, S. of Laem Son, Phuket Id. (ANSP). VIETNAM: Cam Ranh Bay (ANSP). COCOS-KEELING ISLANDS: N. end of Pulo Siput; West Id., Cocos Id. (both ANSP). CHRISTMAS ISLAND: (Tomlin, 1935, p. 79). INDONESIA: Jesselton district, N. Borneo; Pulau Boenta, off Aceh Head, N. W. Sumatra; Sulau Bay, Batu group, off Sumatra; Mega, Mentawai Ids., S. W. Sumatra (all USNM); Queen's Bay,

off Sukabumi, Java (AMNH); Keledjitan, Bantam, Java (ANSP); Batjan Id.; Manipa Id., W. of Halmahera Id.; Mandidi Id.; Ambayana Id., all Moluccas (all MCZ). PHILIPPINES: Corregidor Id.; Manila Bay, Luzon Id.; Calapan, Mindoro Id.; Gigmoto, Catanduanes Id.; Cuyo Id., Palawan group (all ANSP); Panay; Silino Id., Mindanao Id. (both USNM); Sanga Sanga Id., Sulu Archipelago (ANSP). FORMOSA (Taiwan): (AMNH); Suo; Karenko; Botan-wan; Ryukyu-Syo; Hoko (all Kuroda, 1941, p. 111). RYUKYU ISLANDS: Hyakuna reef (AMNH); Yomitan reef, Okinawa; Bolo Point; Kuzu-Saki, all Okinawa (all ANSP); NE coast of Iheya Shima (ANSP); Miyako (FMNH). JAPAN: Kikaiga Shima, Osumi; Oshima Osumi (MCZ); USNM); Tosa (ANSP); Kii, Honshu (FMNH). MARIANAS: Maug; Agnhan (both USNM); Saipan; Tinian; Guam (all AMNH). PALAU ISLANDS: Babelthnap (ANSP); Koror; Eil Malk (both USNM). CAROLINE ISLANDS: Kayangel; Angulapel; Gorokoru; Ngargersiu (all ANSP); Yap (USNM); Ulithi; Italik; Elato; Satawal; Ponape; Kapingamarangi (all ANSP). MARSHALL ISLANDS: Eniwetok Atoll; Rongelap Atoll; Majuro Atoll; Ujae Atoll; Uterik Atoll (all USNM); Bikini Atoll; Arno Atoll (both AMNH). WAKE ISLAND: (AMNH; ANSP; MCZ). NEW GUINEA: Schouten Ids.; Wewak; Makiri reef, Unea Id. (all ANSP); 2 mi. N. of Gusika, 13 mi. N. of Finschhafen (MCZ). ADMIRALTY ISLANDS: Korumi Id. (ANSP). AUSTRALIA: Queensland: Herald Cay, Coral Sea; Pipon reef near Cape Melville (both ANSP); Wilson Id., Capricorn group (MCZ); Lady Elliot Id. (ANSP; AIM); Heron Id. (AIM); Tryon Id., Capricorn group (Powell coll.); Northern Territory: Darwin (FMNH); New South Wales: Middleton reef, off coast of New South Wales (Iredale, 1937, p. 256); Lord Howe Id. (AMS); West Australia: Barrow Id. (Wilson & Gillett, 1971, p. 92). NEW BRITAIN: Rabaul Harbour (ANSP). NEW IRELAND: Kavieng (AMNH). SOLOMON ISLANDS: NW Bougainville Id. (ANSP); Lutee, Choiseul Id.; Ataa, N. Malaita Id.; Lunga, Guadalcanal; Bellona Id. (all AMNH); Tikopia Id. (AIM); Bougainville; Bunama (both Powell coll.). NEW HEBRIDES: Tonga, Espiritu Santo Id. (MCZ); Bushmen's Bay, E. Malekula Id. (AIM); Tanna Id. (DM). NEW CALEDONIA: Touho (AMNH); Isle of Pines (MCZ). LOYALTY ISLANDS: Lifu (USNM). FIJI ISLANDS: Savusavu, Vanna Levu (AMNH); Korolevu, S. Viti Levu (ANSP); Nananu-i-Ra Id., N. Viti Levu (WOC coll.); Ongea Levu, Lau Ids. (USNM). GILBERT ISLANDS: Onotua Atoll (MCZ); Kingsmill Id. (USNM); Nauru Id. (Hedley, 1903, p. 4). ELLICE ISLANDS: Funafuti (AMS; AIM). WALLIS ISLANDS: Nukuhifala (USNM). TONGA ISLANDS: Hufagalupe, Tongatapu (ANSP); Niuafo'ou Id. (USNM). SAMOA ISLANDS: Asat Harbour,

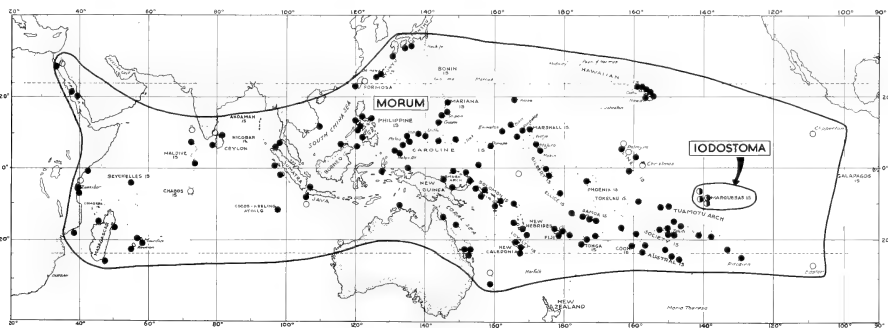


Plate 12. Geographical distribution of *Drupa morum* Röding, and its Marquesan subspecies *D. (D.)*

morum iodostoma (Lesson). Open circles are literature records.

Savaii; Pago Pago, Tutuila (both USNM); Apia, Upolu (AMNH; AIM). NIUE ISLAND: Alofi (USNM); Oneone reef; Namoui reef (both AMNH). PHOENIX ISLANDS: Canton Id. (ANSP). COOK ISLANDS: Bird's Id.; North Id.; both Palmerston Atoll (both USNM); Aitutaki; Mauke; Rarotonga; Mangaia (all USNM); Kopuano Passage, Aitutaki (AIM). PENRRHYN ISLAND: (AMNH; AIM). AUSTRAL ISLANDS: Tubuai; Raivavae; Rurutu (all USNM). SOCIETY ISLANDS: many localities on Bora Bora; Huahine; Moorea; Tahiti (all USNM); Venus Point, Tahiti (AMNH). TUAMOTU ISLANDS: Tikahau Atoll; Vahitahi; Fakarava; Nengonengo; Makatea (all USNM). GAMBIER ISLANDS: Mangareva (USNM). LINE ISLANDS: Palmyra Id. (USNM); Fanning Id. (AMS); Caroline Id.; Flint Id. (both ANSP); Jarvis Id. (Powell coll.); Kingman reef; Washington Id.; Christmas Id. (all Kay, 1971, p. 275). HAWAIIAN ISLANDS: Kamilu, Kauai; Hanauma Bay, Oahu; Pukoo, Molokai; Honokowai reef, Maui; Hilo, Hawaii (all USNM); Kona, Hawaii (AMNH); Koko Head, Oahu; Waikiki, Honolulu (both Powell coll.). PITCAIRN ISLAND: (AMNH). EASTER ISLAND: (Steele, 1957, p. 112). CLIPPERTON ISLAND: (Hertlein & Allison, 1960, p. 15).

Fossil records—HAWAIIAN ISLANDS: Pleistocene: Oahu (Ostergaard, 1928, p. 6; Kosuge, 1969, p. 786, pl. 5, fig. 93).

Drupa morum iodostoma (Lesson, 1840)

(Pl. 2, figs. 4, 5; Pl. 13)

Range—Marquesas Islands.

Remarks—The lack of tubercles, the more quadrate shape, the dark dorsal bands and the pinkish violet aperture distinguish this uncommon subspecies from the nominate species *Drupa morum* Röding.

Early records from both literature and specimens are from numerous localities in the western Indo-Pacific, but reliable data indicate this taxon to be restricted to the Marquesas Islands. Records based on old collections in the National Museum of Natural History, Washington, and the Museum of Comparative Zoology, Harvard, can be confidently dismissed as being based on erroneous locality data, probably copies from locality indications given in old literature; these localities are "Malacca," "New Zealand," "Madagascar" and "Fiji Islands." However, there are several records of "*D. iodostoma*" from neighbouring areas to the Marquesas, such as Palmyra Island in the Line Islands (SDNHM), Venus Point, Tahiti (AMNH) and Fakarawa Atoll, Tuamotus (ANSP); in addition, the subspecies has also been reported in literature from Marutea Island (Couturier, 1907) and Makatea Island (Boettger, 1918), both in the Tuamotu Archipelago. The literature records are suspected

misidentifications, while the actual specimens in the mentioned institutions have either been obtained through secondhand or have been documented by persons who also collected in the Marquesas Islands apart from the Tuamotus. Confirmed, recent collections suggest, therefore, that *D. iodostoma* is an allopatric subspecies of *D. morum*, and is endemic to the Marquesa Islands where *D. morum* is not known to occur.

Habitat—In surge channels cut into exposed volcanic shores (G. D. Stout, personal communication), and in rocky crevices at a depth of 10 feet.

Description—Shell 32 to 47 mm (about 1¼ to 2 inches) in length, quadrately globose, spire very short and acuminate. Whorls faintly axially plicate, spirally ribbed by five wide, slightly raised ribs which are more pronounced toward the margin. Interstices between ribs striated with 3 lirations. Aperture narrow, linear, extending nearly three-quarter the length of the shell. Outer lip crenulated between ribs, inner margin dentate; teeth compound, 3 to 4 denticles in the upper tooth, 2 to 3 denticles in the lower tooth. Above the anterior canal are two conspicuous plaits. Columella with three to four heavy plications projecting into the aperture. Posterior siphonal canal elongate, obliquely curved toward the apex. Color cream, spiral ribs brownish black, interstitial spiral threads reddish brown; aperture pinky-violet.

The radula is similar to *Drupa morum*; the rachidian has bifid side-cusps and 4 or 5 lateral denticles. The radula of "*Drupa iodostoma*" as figured by Cooke (1919) from the "Sandwich Islands" [= Hawaiian Ids.], is probably based on Hawaiian specimens of *D. morum*.

Measurements (mm)—(all specimens with a mature lip).

length	width
47.0	43.0 Nukuhiva, Marquesas Ids.
38.0	36.5 Nukuhiva, Marquesas Ids.
36.0	32.7 Tahuata, Marquesas Ids.
30.3	27.0 Tahuata, Marquesas Ids.

Synonymy—

- 1840 *Purpura* (*Ricinus*) *iodostoma* Lesson, Rev. Zool. Soc. Cuvierienne, vol. 3, p. 355 ("New Zealand" = error!).
 1842 *Purpura iodostoma* Lesson, Guérin's Magasin de Zoologie, vol. 4, p. 58, pl. 58.



Plate 13. Radula of *Drupa (Drupa) morum iodostoma* (Lesson). Half a transverse row; Tahuata, Marquesa Ids.

- 1846 *Ricinuia iodostoma* Lesson, Reeve, *Conchologia Iconica*, vol. 3, pl. 1, figs. 4a, b; 1860 Reeve, *Elements of Conchology*, vol. 1, p. 82, pl. 7, fig. 32; 1880 Tryon, *Manual of Conchology*, vol. 2, p. 184, pl. 56, fig. 199.
- 1888 *Ricinuia iodostoma* (sic) Lesson, Paetel, *Catalog der Conchyl-Sammlung*, vol. 1, p. 143 (New Zealand [erroneous]).
- 1908 *Pentadactylus (Pentadactylus) iodostomus* Lesson, Horst & Schepman, *Cat. Syst. Moll. Mus. Hist. Nat. Pays-Bas*, vol. 13, p. 154.
- 1913 *Drupa iodostoma* Lesson, Hedley, *The Nautilus*, vol. 27, no. 7, p. 80; 1957 Kaicher, *Indo-Pacific Sea Shells*, pl. 4, fig. 5 (Malaysia and Melanesia [= error!]); 1965 Hertlein, *Occ. Papers California Academy of Sciences*, no. 49, p. 2, figs. 1, 2 (Marquesas Islands).
- 1918 *Ricinuia iodostoma* (sic) Lesson, Boettger, *Abh. Senckenb. Naturfr. Gesellschaft*, vol. 36, (3), p. 298 [Probably misidentified *Drupa morum* Röding].

Types—The type-specimen of *Drupa iodostoma* (Lesson) is probably in the Muséum National d'Histoire Naturelle, Paris. The given locality "New Zealand" is erroneous, as the species does not live there. Since the type-specimen was collected during the voyage of the "Vénus," which visited the Marquesas

after the 14th of August, 1838, and also called at the Bay of Islands, New Zealand, during October 1838 (Chamberlin, 1960, p. 67), the erroneous locality is obviously due to a mix-up of specimens during the voyage. Since reliable records are known only from the Marquesas, we designate Taiohae, Nukuhiva Island, Marquesa Islands, as the type locality of *D. morum iodostoma*.

Records—MARQUESAS ISLANDS: Hana Nui and Haavie Bays, Ua Huka Id.; Eiao Id. (all ANSP); Taiohae, Nukuhiva Id. (USNM; AMNH); N. side Hana Moe Noe Bay, Tahuata (USNM).

Drupa ricinus ricinus (Linnaeus*, 1758)

(Pl. 2, figs. 6-8, 11; Pls. 14, 15, 16)

Range—From East and South Africa to the Eastern Pacific, at Easter, Clipperton and Galapagos Islands.

Remarks—Differs from *D. morum*, which has a proportionally larger shell, in having longer spines, a smaller size and in lacking the purple or mauve apertural coloration. *D. elegans* (Broderip & Sowerby) differs mainly by possessing a continuous, red-brown line encircling the aperture; it is restricted to Polynesia where it is found with the present species.

*It is the editorial policy to allow authors to use their own preference in spelling this name. Linnaeus or Linne.

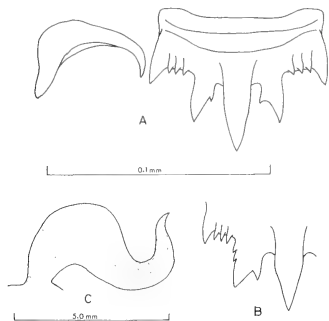


Plate 14. *Drupa (Drupa) ricinus ricinus* (Linnaeus)—white mouthed form; Fiji Islands.
Fig. A. Radula; half a transverse row.
Fig. B. Part of rachidian of radula showing variation in the number of accessory denticles on the side-cusps.
Fig. C. Penis.

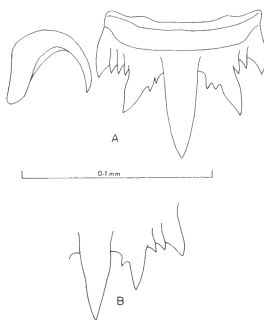


Plate 15. *Drupa (Drupa) ricinus ricinus* (Linnaeus)—yellow mouthed form; Fiji Islands.
Fig. A. Radula; half a transverse row.
Fig. B. Part of rachidian of radula showing variation in the side-cusps and lateral denticles.

Commonly, *D. ricinus* may have a faint orange or yellow, diffused line encircling the aperture.

Populations with large shells, attaining nearly 40 mm in length, are present in the Red Sea. This form appears to be geographically isolated from the smaller-shelled, nominate subspecies, and it is recognized herein as a new subspecies *Drupa ricinus hadari*.

Habitat—Lives exposed, or in water up to approximately 10 feet deep, on or under rocks, sand, weed or coral, on exposed wave benches or fringing reefs. At Clipperton Island the species has been collected to a depth of 22 fathoms.

Description—Shell 17 to 35 mm (about $\frac{3}{4}$ to 1½ inches) in length, solid, obovoid, spire short, reduced, obscure in adult specimens, body whorl three-quarter the length of the shell. Whorls ribbed with five rows of sharp spines; spines variable in development, but higher near the margin of the aperture. Interstices between spines striated with scale-like striae. Aperture linear, constricted by the teeth and callus. Apertural dentition as in *D. morum* with features less prominent. Color white or grayish; spines dark-brown to dark-gray, especially toward the tips; mouth white or with a wide, broken, diffused, orange to yellow line extending around the outer lip and neighbouring canal area. Operculum typical for the group.

In the radula, the side-cusps of the rachidian are short or moderately long, bifid to quadrid, and are followed by 2-3 side-denticles, exclusive of the end-cusps.

Measurements (mm)—(including spines; all specimens with a mature lip).

length	width	
32.3	27.8	Kagoshima, Japan
29.5	25.5	Lectotype of <i>arachnoides</i> Lamarck
25.6	27.0	S. Viti Levu, Fiji Ids.
23.0	25.0	Probable holotype of <i>ricinus</i> Linnaeus
22.8	21.0	Penrhyn Id.
17.2	16.3	Samarai, Papua

Synonymy—

- 1705 ——— Rumphius, Amboinsche Rariteitskammer, pl. 24, fig. E.
- 1742 ——— d'Argenville, L'Histoire Naturelle , pl. 17, fig. A.
- 1742 ——— Gualtieri, Ind. test. Conchyliorum, pl. 28, fig. N (poor).
- 1758 *Murex ricinus* Linnaeus, Systema Naturae, ed. 10, p. 750 (refers to Rumphius and Gualtieri, *op. cit.*) [Asiatic Ocean] (yellow and white forms).
- 1758 *Murex hystrix* Linnaeus, Systema Naturae, ed. 10, p. 750 (refers to d'Argenville, *op. cit.*) [no locality given] (juvenile specimen); 1855 Hanley, Ipsa Linn. Conch., p. 294.
- 1777 "*Murex Morum globosum*" Martini, Syst. Conchyli-Cabinet, vol. 3, p. 280, pl. 102, figs. 976, 977 (non binomial) [yellow form].
- 1798 *Drupa tribulus* Röding, Museum Boltenianum, p. 55 (refers to Rumphius and Gualtieri, *op. cit.*) [no locality given].
- 1798 *Drupa rubuscaesius* Röding, *ibid.*, p. 55 (refers to Martini, *op. cit.*) [no locality given] (yellow form).
- 1810 *Sistrum album* Montfort, Conchyliologie Systématique, vol. 2, p. 595, fig. on p. 594 (white form) [no locality given].
- 1816 *Ricnula arachnoides* Lamarck, Tableau Encyclopédique Méthodique, p. 1, pl. 395, figs. 3a, b (no locality given) [yellow form]; 1822 Lamarck, Hist. nat. anim. s. vertébrés, vol. 7, p. 232 (Indian Ocean); 1823 Sowerby, Gen. Rec. fossil shells, pt. 18, pl. 235, fig. 5 (juvenile specimen); 1842 Reeve, Conchologia Systematica, vol. 2, p. 215, pl. 256, fig. 5 (juvenile specimen); 1846 Reeve, Conchologia Iconica, vol. 3, pl. 1, fig. 5; 1859 Chenu, Manuel de Conchyliologie, vol. 1, p. 168, fig. 812.
- 1831 *Murex neritoides* Mawe, Wodarch's Intr. Conchology, pl. 3, fig. 43 (yellow form) [non Linnaeus, 1767].
- 1832 *Purpura albo-labris* Blainville, Nouv. Ann. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 208, pl. 9, fig. 5 (Trincomalee, Ceylon) [white form]; 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 12, pl. 1, fig. 2.
- 1832 *Purpura arachnoides* Blainville, *ibid.*, p. 209 (yellow form); 1833 Quoy & Gaimard, Voyage l'Astrolabe, vol. 2, p. 579, pl. 39, figs. 17-19 (animal and operculum); 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 10, pl. 1, figs. 3, 3a; 1848 Krauss, Südafrik. Mollusken, p. 115 (Natal).
- 1850 *Sistrum arachnoides* Lamarck, M. Gray, Figs. Moll. Animals, vol. 4, p. 70, pl. 96, fig. 2.
- 1853 *Pentadactylus ricinus* Linnaeus, H. & A. Adams, Gen. Rec. Mollusca, vol. 1, p. 130; 1875 Troschel, Gebiss der Schnecken, vol. 2, p. 134, pl. 13, fig. 5 (radula).
- 1859 *Ricnula abolabris* Blainville, Chenu, Manuel de Conchyliologie, vol. 1, p. 168, fig. 812.
- 1880 *Ricnula ricinus* Linnaeus, Tryon, Manual Conchology, vol. 2, p. 184, pl. 56, fig. 200 and pl. 57, figs. 204, 206, 212; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 240.
- 1884 *Pentadactylus arachnoides* Lamarck, Fischer, Manuel de Conchyliologie, fasc. 7, p. 646, pl. 6, fig. 9.
- 1911 *Sistrum ricinus* Linné, Schepman, Siboga-Expeditie, vol. 49d, p. 354.
- 1913 *Drupa ricinus* Linné, Hedley, Nautilus, vol. 27, no. 7, p. 80; 1937 Hertle, Proc. Amer. Phil. Society, vol. 78, no. 2, p. 308, pl. 1, figs. 5, 6 (Clipperton and Galapagos Ids.); 1967 Orr Maes, Proc. Acad. Nat. Sci. Philadelphia, vol. 119, no. 4, p. 129; 1969 Cernohorsky, Veliger, vol. 11, no. 4, p. 299, pl. 47, figs. 8, 8a (shell), text figs. 5, 6 (radula); 1970 Salvat, Cahiers du Pacifique, no. 14, p. 46; 1971 Kay, Pacific Science, vol. 25, pp. 266, 275; 1971 Wilson & Gillett, Australian Shells, p. 92, pl. 61, figs. 3, 3a.
- 1915 *Drupa rubus-cestus* Dall, Smithsonian Inst. Publ. no. 2360, p. 29 (refers to Röding, 1798, p. 55, species 695 = *D. tribulus* Röding).
- 1929 *Drupa (Drupa) ricinus* Linnaeus, Thiele, Handb. syst. Weichtierkunde, vol. 1, p. 295; 1938 Adam &

Leloup, Mém. Mus. Roy. d'Hist. Nat. Belg., vol. 2, fasc. 19, p. 164.

- 1933 *Ricinus ricinus* var. *arachnoides* Lamarck, Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 240.
- 1960 *Drupa ricina* Linnaeus, Hertlein, Veliger, vol. 3, no. 1, p. 8; 1965 Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 115, pl. 13, fig. 1 (radula); 1965 Wu, Bull. Inst. Zool. Acad. Sinica, vol. 4, p. 98, text fig. 18 (radula); 1965 Wu, Malacologia, vol. 3, no. 2, p. 211, text figs. (anatomy).
- 1960 *Drupa ricina* forma *albolabris* Blainville, Hertlein, Veliger, vol. 3, no. 1, p. 8.
- 1965 *Drupa albolabris* (Blainville), Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 114, pl. 13, fig. 2 (radula).
- 1965 *Drupa arachnoides* Lamarck, Wu, Bull. Inst. Zool. Acad. Sinica, vol. 4, p. 98, text fig. 18 (radula).

Types—The probable type-specimen of *Drupa ricinus* (Linnaeus) [Pl. 16, fig. 2], is in the Linnean collection of the Linnean Society, London. This particular specimen is the yellow-spotted form, which has a no. 540 written on the columella (the number of *Murex ricinus* in the 12th edition of the "Systema Naturae"). Two additional, undocumented specimens are also in the collection, an adult of the white form and a juvenile specimen. Five syntypes of *Ricinus arachnoides* Lamarck, are in the Muséum d'Histoire Naturelle, Geneva, and the 29.5mm long syntype, no. 1101/15/4, is here selected as the lectotype (Pl. 16 fig. 4). The type-specimen of *Purpura albolabris* Blainville, is probably in the Muséum National d'Histoire Naturelle, Paris. The type locality of *D. ricinus* is "Asiatic Ocean," which is here restricted to Ceylon (specimens in MCZ, ANSP and AMNH).

Nomenclature—Much confusion has existed regarding the identity of this taxon. Lamarck, 1822, considered *Murex hystrix* Linnaeus, to be the pink-apertured species which is correctly known as *Drupa rubusidaeus* Röding. This misconception was continued by many early authors. Actually, as is pointed out by Hanley (1855), Linnaeus referred Regenfuss' (1758) excellent colored figure of *Drupa rubusidaeus* Röding to *Murex hippocastanum* in his 12th edition of the "Systema Naturae," and not to *Murex hystrix*. In the 10th edition, the short diagnosis of *Murex hystrix* was accompanied by only one figure reference, pl. 17, fig. A of d'Argenville, 1742. This engraving (see Pl. 16 fig. 1) unmistakably represents the dorsal aspect of *Drupa ricinus* as indicated by the long, obliquely slanted spines which characterize some forms of this species. In the description Linnaeus states: "apertura edentula repanda,"



Plate 16. *Drupa (Drupa) ricinus ricinus* (Linnaeus).

Fig. 1. Lectotype figure of *Murex hystrix* Linnaeus, from d'Argenville, 1742, L'Histoire Naturelle . . . Conchyliologie, pl. 17, fig. A.

Fig. 2. Probable type-specimen of *Murex ricinus* Linnaeus, from the "Asiatic Ocean" (Linnean Society of London coll.; 23.0 x 25.0 mm).

Fig. 3. Lectotype figure of *Drupa rubuscaesius* Röding, from Martini, 1777, Syst. Conchylien-Cabinet, vol. 3, pl. 102, fig. 976.

Fig. 4. Lectotype of *Ricinus arachnoides* Lamarck (MHNG no. 1101/15/4; 25.5 x 29.5 mm).

an indication that this species was based on specimens in which the dentate lip has not yet developed. Thus it can be safely assumed that *Murex hystrix* Linnaeus, is nothing more than a juvenile of *Drupa ricinus* Linnaeus.

At the present time, some students recognize two species, the form with a white aperture as *Drupa albolabris* (Blainville) and the yellow-orange spotted form as *D. arachnoides* (Lamarck). The latter should not be confused with the yellow-mouthed *D. grossularia* Röding. In a detailed sampling of *D. ricinus* in the Fiji Islands by the junior author (Cernohorsky, 1969), both

forms were found not only to be sympatric in various localities, but were sharing the same rock in many instances. No sexual dimorphism was observed in either color form, and no differences in either living animal, radula, color of the stomach pouch or the penis were apparent in either form. The number of accessory side-denticles in the rachidian of the radula varied from 3 to 5 in both color forms. Both color forms of *D. ricinus* have been collected together at various other Indo-Pacific localities. Hertlein and Allison (1960) recorded the presence of both color forms of *D. ricinus* at Clipperton Island, an isolated coral atoll in the eastern Pacific, located about 670 miles southwest of Acapulco, Mexico. The white-apertured form was reported to be living among boulders and coral debris on the outer parts of the reef flats, and off the edge of the reef flats, in coral and coral rubble, to a depth of at least 130 feet, the lower limit of collecting by their SCUBA divers. Although the white-apertured form was found in abundance, only abraded specimens of the yellow-orange form were on the beach and off shore at a depth of 70 feet. In the New Hebrides the white-mouthed form only was found by the junior author.

Records—(inserted in brackets: y = yellow-spotted form, w = white form). GULF OF ADEN: Aden (Shopland, 1896, p. 220). EAST AFRICA: Isla di Serpenti, Chisimaio, Somalia (AMNH; yw); Port Amelia, Mozambique (AMNH; y); Kendwa Id., 4 mi. ESE Dar-es-Salaam, Tanzania; Pangavini Id., 10 mi. NNE Dar-es-Salaam, Tanzania; Ras Kankadya, 6 mi. N. Dar-es-Salaam, Tanzania (all MCZ; y); Diani Beach, Kenya (AMNH; USNM; y); Mombasa, Kenya (AMNH; y). ZANZIBAR: (AMNH; w); Ras Nyngwe, Chumbe Id.; Jembiani, 5 mi. S. Paje; Kiwenga (all ANSP; y). SOUTH AFRICA: Umtwahnini, 22 mi. N. Port Shepstone, Natal; East London (both ANSP; y). SEYCHELLES: Loraie Bay, Curieuse Id.; Anse aux Pins (both ANSP; y); Coetivy Id.; Praslin Id. (Mel-

vill, 1909, p. 103). MADAGASCAR: Ambodifototra, Isle St. Marie (MCZ; w); N. E. of Pointe Antsiraikiraky, NW Isle St. Marie; Ambariobe, S.E. Nossi Bé; Grande Recife, Tulear; Pointe Ibanona, Fort Dauphin (all MCZ; y). REUNION: (ANSP; w). MAURITIUS: Pointe Fayette; S.W. Port Louis (both ANSP; w); 1 mi. NW Black River Atoll; y). MALDIVE ISLANDS: Ongu Id., N. Malosmadulu Atoll; Wala Id., Nilandu Atoll; Fadifolu Atoll (all ANSP; y); Imma Id., N. Male Atoll (ANSP; w). CEYLON: (MCZ; w); Pointe de Gallet (ANSP; y); 12 mi. N. of Trincomalee (AMNH; y). ANDAMAN ISLANDS: (Melville & Sykes, 1899, p. 222). THAILAND: Laan Seng, 1 mi. S. Laan Son, Phuket Id. (ANSP; y); Goh Huyong, Similan Ids. (USNM; y). VIETNAM: Con Son Ids. (Fischer, 1891, p. 149). COCOS-KEELING ISLANDS: Direction Id. (ANSP; y); E. side of Horsburgh Id.; SW side West Id. (both ANSP; y). CHRISTMAS ISLAND: (Tomlin, 1934, p. 79). INDONESIA: Pulau Bai, Batu group, off Sumatra; Pulau Stupai, Mentawai Ids., S.W. Sumatra; Pelaboean Race, Preanger, Java (all USNM; y); Morotai Id., Moluccas (MCZ; y); Mantanani Id. and Mandi Darrah Id., N. Borneo (both ANSP; y); Batu Dua and Pulau Pombu, Wasi, Ambon I. (both FMNH; y); Malawali, N. Borneo (AMNH; y). PHILIPPINES: Many localities throughout the Archipelago; Luzon Id. Mindoro Id.; Cebu Id.; Sulu Archipelago (AMNH; ANSP; y); Samar Id.; Catanduanes Id.; Palawan Id. (AMNH; ANSP; yw); Calamianes group; Mindanao Id. (AMNH; ANSP; MCZ; w); Borongan village, Samar Id.; Gig-moto, Catanduanes Id. (both AIM; yw). FORMOSA (Taiwan): Tainan beach (AMNH; w); Suo; Kasyo-to; Botanwan; Ryukyu-syo; Hoko (Kuroda, 1941, p. 111; y); Karenko; Lasyoto; Garanihi; Hoko; Ryukyu-syo (Kuroda, 1941, p. 111; w). RYUKYU ISLANDS: Kikaiga Shima (ANSP; y); Bolo reef, NW Nakagami Gun, Okinawa (USNM; y); Okuma, Kuni-gami-Gun; Odomari, Okinawa (both USNM; w); Yonitan reef, Okinawa (AMNH; yw). JAPAN: Oshima, Osumi (USNM; yw); Hachijo Id., off Honshu (ANSP; w); Tosa, Shikoku (ANSP; y); Kagoshima, Kyushu (ANSP; w). MARIANAS: Lagunan Tanapaa, Saipan; Agat Bay, Guam (both ANSP; y); Apra Harbour, Guam (AMNH; y); Tinian Id. (FMNH; yw); several localities on Guam Id. (USNM; w); Saipan (AMNH; w). PALAU ISLANDS: Angupelu Id., SE Koror Id.; reef N. of Gorokottan Id., S. side W. Passage, Babelthup Id. (both ANSP; y); S. E. of Auropushekaru Id., Malakal Harbour, Koror Id. (ANSP; yw); Angaur, Peleliu Id. (FMNH; w). CAROLINE ISLANDS: N. of Kayangel Id.; S. of Garakayo Id.; Ponape; Yap (all ANSP; y); Ulithi Atoll; Satawal Atoll; Manini, Kapingamarangi (all USNM; y); S.E. Rattakadokoru Id. (ANSP; w). MARSHALL ISLANDS: Eniwetok Atoll; Kwajalein Atoll (both AMNH; y); Bikini Atoll; Eniwetok Atoll; Rongelap Atoll; Rongerik Atoll; Kwajalein

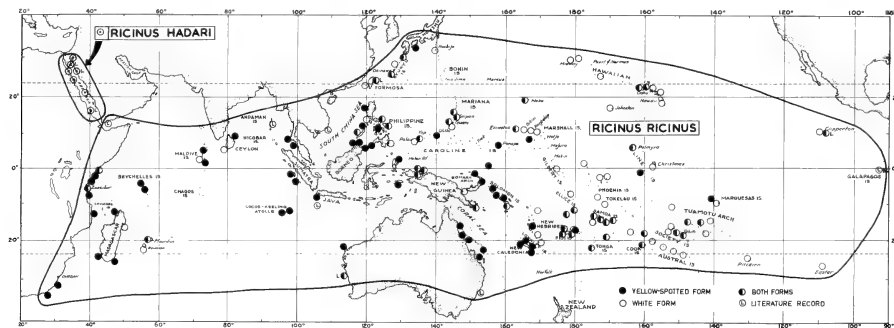


Plate 17. Geographical distribution of *Drupa (Drupa) ricinus ricinus* (Linnaeus) in the Indo-Pacific, and its subspecies

D. (D.) ricinus hadari Emerson and Cernohorsky, in the Red Sea.

Atoll (all ANSP; w). WAKE ISLAND: (AMNH, yw; ANSP, y). NEW GUINEA: NE Noekori Id.; Manokwari; SW Biak dock, Biak Id. (all ANSP; y); Boensaki Id., off Soweik, Soepiri Id., Schouten Ids. (ANSP; yw); NE Mioses Woendi, Padaido Ids. (ANSP; yw); Samarai, Papua (AMNH; yw); Huon Gulf (USNM; y). AUSTRALIA: Queensland: Capricorn Ids.; Hardy reef, Great Barrier reef (both AMNH; y); Birds Id.; Green Id., Cairns (both USNM; y); Magnetic Id.; Lady Elliot Id. (both AIM; y); New South Wales: (Iredale & McMichael, 1962, p. 74); West Australia: Vlaming Head (FMNH; y); Houtman, Abrolhos Archipelago (Wilson & Gillett, 1971, p. 92). NEW BRITAIN: Rabaul Harbour (ANSP; y). NEW IRELAND: Kavieng (AMNH; y). SOLOMON ISLANDS: Kieta, Bougainville; Lutee, Choiseul Id.; Ataa, N. Malaita Id.; Tulagi Id.; Santa Ana Id. (all AMNH; y); Tikopia Id. (AIM; w); Lunga, Guadalcanal (AMNH; yw). NEW HEBRIDES: Lamap, Malekula Id. (ANSP; w); Bushmens Bay, E. Malekula Id. (AIM; w); Pango Point, Efate Id. (AIM; w); Tauna Id. (DM; w). NEW CALEDONIA: SE Dumbes Pass, off Noumea; Baie Quemo, Noumea; Koe, Touho (all ANSP; y). LOYALTY ISLANDS: Lifu (USNM; y). GILBERT ISLANDS: Abemama (USNM; w). ELLICE ISLANDS: Funafuti lagoon (USNM; AIM; w). WALLIS & FUTUNA ISLANDS: Faioa; Uvea; Nukuhifala, all Wallis Id. (USNM; y); Nukuhifala, Wallis Id. (USNM; w); Anse de Sigave, Futuna Id. (USNM; y); Mua, Alofi, Hoorn Id. (USNM; y). FIJI ISLANDS: Koro Bay reef, Vanua Levu (AMNH; y); Suva Harbour, S. Viti Levu (USNM; y); Korolevu, S. Viti Levu; Yasawa reef (both AMNH; w); Namagumaga village, S. Viti Levu (WOC coll.; w); Rat Tail Passage, Suva reef, S. Viti Levu; Mamanuca group; Cabori beach; Manava Id.; Nanam-i-Ra Id.; Viti Levu Bay, all Viti Levu (all WOC coll.; yw). TONGA ISLANDS: Ha'ateiho reef, Tongatapu; E. coast Tongatapu Id. (both USNM; y); Haakoma, Tongatapu (MCZ; w); Hufagehupe, Tongatapu (MCZ; yw) Niuafo'ou Id. (USNM; w). NIUE ISLAND: near Malatu (USNM; y); Oneone reef (AMNH; y); Alofi (USNM; yw). SAMOA ISLANDS: Vailele Bay, Upolu; Tafuna, Tutuila (both ANSP; y); Fagaitua Bay, Tutuila; Ofu (both MCZ; w); Asau Harbor, Savaii (USNM; yw); Apia, Upolu (AMNH; yw); Tau Iid., Manua group (MCZ; yw). TOKELAU ISLANDS: W. side Tuku, Manihiki Atoll (ANSP; w); Swains Id. (USNM; w). PHOENIX ISLANDS: Canton Id.; Enderbury Id. (both USNM; y). HOWLAND ISLAND: (USNM; w). COOK ISLANDS: Bird's Id., Tom's Id.; North Id., all Palmerston Atoll (all USNM; w); Koromiri Id., SE Rarotonga (ANSP; y); several localities on Aitutaki; Mauke; Rarotonga; Mangaia (all MCZ; USNM; w); Motu Akaiaia, Aitutaki (USNM; yw). AUSTRAL ISLANDS: Rurutu; Tubuai; Raiivavae (all USNM; w). SOCIETY ISLANDS: Mopelia Id. (ANSP; y); many localities on Bora Bora; Huahine; Raiatea; Moorea; Tahiti (USNM; w); Arue, Tahiti; Taone, Tahiti; Huahine (all USNM; yw). TUAMOTU ISLANDS: Napuka (AMNH; w); Tatumae; Clermont Tenere; Takaroa (all ANSP; w); Rangiroa (AMNH; yw); Mangareva (AMNH; w); Raroia (ANSP; yw). PITCAIRN ISLAND: (AMNH; USNM; w). MARQUESAS ISLANDS: Taiohae, Nukuhiva (AMNH; y); Hiva Oa Id. (ANSP; w); Ua Huka Id. (AMNH; ANSP; w). LINE ISLANDS: Christmas Id.; Flint Id.; Palmyra Id. (all ANSP; w); Palmyra Id. (MCZ; y); Jarvis Id. (AMNH; y). JOHNSTON ISLAND: (USNM; w). HAWAIIAN ISLANDS: Honolulu Harbour (ANSP; y); Kure Id.; Midway Id.; Laysan Id.; Tern Id.; French Frigate Shoal; Kauai Id.; Oahu Id.; Molokai Id.; Maui Id.; Hawaii Id. (all AMNH; ANSP; USNM; w); Niihau Id.; Oahu Id. (both AIM; w); Lihue, Kauai (AMNH; yw). CLIPPERTON ISLAND: (AMNH; ANSP; w); (Hertlein & Allison, 1960, p. 15; yw). GALAPAGOS ISLANDS: (Hertlein, 1960, p. 8).

Fossil records— ZANZIBAR: Pleistocene: Base of well, village W. of Makunduchi (Cox, 1927, p. 90, pl. 18, figs. 12a, b and Stockley, 1928, p. 79). MOZAMBIQUE: Pleistocene: Chidenguel, Inhambane district (Cox, 1939, p. 90). HAWAIIAN ISLANDS: Pleistocene: Oahu (Mansfield in Stearns and Vaksvik, 1935, p. 167; Kosuge, 1969, p. 786, pl. 5, fig. 90).

Drupa ricinus new subspecies hadari Emerson and Cernohorsky

(Pl. 2, figs. 9, 10; Pl. 18)

Range—Red Sea only.

Remarks—Distinguished from the nominate subspecies *Drupa ricinus* (Linnaeus) by its larger size, heavier shell and more strongly developed parietal shield.

Habitat—Coral reefs and rocks, on intertidal reef-flats.

Description—Juveniles typical of those of both apertural color forms of the nominate subspecies, with spinose nodules dark brown. Nodules on the body whorl or mature specimens white, with brown nodules on spire only, or body whorl axially streaked with brown except on the last two or three rows of spines. Aperture in mature specimens white with fully developed parietal shield completely concealing nodular coloration of the parietal area.

The side-cusps of the rachidian of the radula are bifid and are followed by 2 weak, short lateral denticles, excluding the slightly longer end-cusps.

Measurements (mm)—(including spines)

length	width	
38.0	34.2	Eilat, Gulf of Aqaba (paratype AMNH no. 112617b)
37.2	38.7	Eilat, Gulf of Aqaba (holotype AMNH no. 166928)
34.2	34.1	Eilat, Gulf of Aqaba (paratype AMNH no. 112617a)
32.0	32.0	Eilat, Gulf of Aqaba (paratype AMNH no. 112617c)
28.0	29.0	Eilat, Gulf of Aqaba (paratype DMNH no. 51119)

Synonymy—

- 1862 *Ricinus albolabris* Blainville, Küster (pars), Syst. Conchylien-Cabinet, ed. 2, Abt. 1E, *Ricinus*, pl. 2, figs. 1, 2 (Red Sea) [non *Purpura albolabris* Blainville, 1832].
1941 *Drupa* (*Drupa*) *ricinus* (Linné), Wenz, Handb. Paläozoologie, vol. 6, pt. 5, p. 1114, fig. 3165 (Red Sea) [non *Murex ricinus* Linnaeus, 1758].

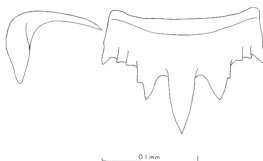


Plate 18. Radula of *Drupa* (*Drupa*) *ricinus hadari* Emerson and Cernohorsky. Half a transverse row; Eilat, Gulf of Aqaba, Israel.

Types—The holotype, AMNH No. 166928, and 8 paratypes AMNH No. 112617, have been deposited in the American Museum of Natural History, New York. Other paratypes are in the Delaware Museum of Natural History, Greenville, The Auckland Institute and Museum and the Tel Aviv University, Israel. The type locality is Eilat, Gulf of Aqaba, Israel.

Nomenclature—The subspecies is named in honor of the late Aryeh Hadar, who kindly submitted specimens from the Gulf of Aqaba for study.

Records—RED SEA: Sharm, Gulf of Suez (DMNH); Eilat, Gulf of Aqaba (AMNH; DMNH; AIM; w); Ras Banas, Egypt (USNM; w); Quseir, Egypt (LACMNH; y); Mualla, Abu Zabad, Gulf of Aqaba (Rees and Stuckley, 1952, p. 196); Suakin, Sudan (Sturany, 1905, p. 141); Jiddah, Saudi Arabia (AMNH; yw); Pointe du Requin, Ile Abulat (Franc, 1956, p. 37).

Drupa elegans (Broderip and Sowerby, 1829)

(Pl. 2, fig. 12; Pl. 19, 20)

Range—From Wake Island to the Tuamotu Islands.

Remarks—This species is similar to *Drupa ricinus* (Linnaeus), but differs in apertural coloration, the lack of tubercle coloring and in being smaller in size. This uncommon species occurs sympatrically throughout its range with *D. ricinus* (Linnaeus). It may prove eventually to be another, moderately rare color phase of that variable species. Although an occurrence of *D. elegans* in the Society Islands is probable, the cited record requires confirmation; specimens from that locality in the Academy of Natural Sciences of Philadelphia and the National Museum of Natural History, Washington, lack exact locality data.

Habitat—Only five specimens were taken by the operation "Crossroads" in 1946 and the biological re-survey in 1947 of the Marshall Islands. These were found living in association with the extremely common yellow-spotted and white color phases of *Drupa ricinus*. On Niue Island, the species is also sympatric with *D. ricinus* and has been collected on reefs under cliff overhangs (D. C. Johnson, personal commun.).

Description—Shell 13 to 25 mm (about $\frac{1}{2}$ to 1 inch) in length, sub-ovate, spire short; body whorl spirally ribbed with five rows of siphonous

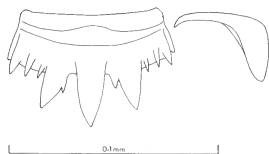


Plate 19. Radula of *Drupa* (*Drupa*) *elegans* (Broderip and Sowerby). Half a transverse row; Vailoa, Alofi Bay, Niue Id.



Plate 20. *Drupa* (*Drupa*) *elegans* (Broderip and Sowerby). Figs. 1, 2. Lectotype from unknown locality (B.M. (N.H.), 20.3 x 22.4 mm) [photo courtesy J. Taylor, B. M. (NH)]. Figs. 3, 4. Specimen from Vailoa, Alofi Bay, Niue Id. (WOC coll.; 19.0 x 20.7 mm).

tubercles. Interstitial surface minutely scaled. Parietal shield moderately enameled, reflected over body wall to form a heavy callus; lower portion of columella 4 plaited. Axial fold strongly developed. Aperture very narrow, dentition of

outer lip as in *Drupa ricinus* (Linnaeus). Color of the exterior and aperture white; aperture encircled by a continuous dark reddish brown line in mature specimens; in juvenile specimens, the line is disrupted and restricted to the columellar lip and near the anal siphonal canal.

Radular ribbon very small, side-cusps of the rachidian bifid, followed by 3 slender and deeply rooted lateral denticles, exclusive of the short end-cusps.

Measurements (mm)—(including spines; all specimens with a mature lip)

length	width	
25.0	25.0	Wake Island
20.3	22.3	Lectotype of <i>elegans</i> B. and S.
19.0	20.7	Niue Id.
18.5	17.5	Lord Hood Id. (S. Marutea Id.)
13.6	11.8	Lord Hood Id. (S. Marutea Id.)

Synonymy—

- 1829 *Ricinuia elegans* Broderip & Sowerby, Zoological Journal, London, vol. 4, p. 376 (no locality given); 1839 Gray, Zool. Capt. Beechey's voyage, p. 155, pl. 36, fig. 4; 1844 Deshayes & Milne-Edwards, Hist. nat. anim. s. vertèbres, ed. 2, vol. 10, p. 52; 1846 Reeve, Conchologia Iconica, vol. 3, pl. 1, fig. 1 (Lord Hood Id. = South Marutea Id.); 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 238.
- 1853 *Pentadactylus elegans* Broderip, H. & A. Adams, Genera Recent Mollusca, vol. 1, pp. 129, 130; vol. 3, pl. 13, figs. 6a, b (operculum only).
- 1880 *Ricinuia ricinus* var. *elegans* Broderip, Tryon, Manual of Conchology, vol. 2, p. 184, pl. 56, fig. 193.
- 1913 *Drupa ricinus* var. *elegans* Broderip & Sowerby, Hedley, Nautilus, vol. 27, no. 7, p. 80.
- 1957 *Drupa elegans* Broderip & Sowerby, Kaicher, Indo-Pacific Sea Shells, (Murexacea, Buccinacea), pl. 3, fig. 18.

Types—Three syntypes of *Drupa elegans* are in the British Museum (Nat. Hist.), and the 20.3mm long syntype (Pl. 20, figs. 1, 2) is here selected

as the lectotype. The species was described from shells in the Museum of the Zoological Society brought home by Lieutenant Belcher who sailed under Captain Beechey in the "Blossom" on its voyage to the Bering Straits and the Pacific (1825-1828). No type locality was given, but Cuming collected it from Lord Hood Island (= S. Marutea Id.), and his specimen was figured by Reeve (1846). Lord Hood Island (= S. Marutea Id.) is here designated as the type locality.

Records—WAKE ISLAND: (BPBM). MARSHALL ISLANDS: Namu Id., N. W. end of Bikini Id., Enman Id., Bikini Atoll, Eniwetok Atoll (all USNM). LINE ISLANDS: Caroline Id.; Flint Id. (both ANSP). NIUE ISLAND: (AMNH); Vailoa, Alofi Bay (D. C. Johnson coll.; WOC coll.); Avatele (S. Herriot coll.). COOK ISLANDS: Akamaru Id., Manihiki Atoll (ANSP). SOCIETY ISLANDS: (ANSP; USNM). TU-AMOTU ISLANDS: Lord Hood Id. (= S. Marutea Id.) (AMNH; BMNH); Vahitahi; Nengonengo Id. (both USNM); Anaa Id. (MCZ); Napuka; Taenga; Fakahina (Dautzenberg & Bouge, 1933, p. 238).

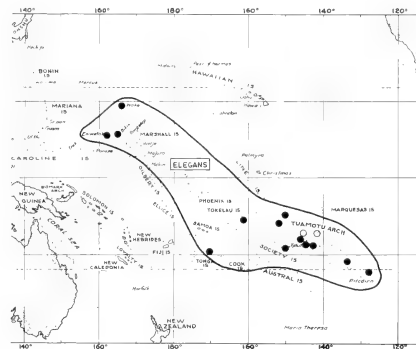


Plate 21. Geographical distribution of *Drupa (Drupa) elegans* (Broderip and Sowerby). Open circles are literature records.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Drupa rubusidaeus Röding, 1798

(Pl. 2, figs. 13-15; Pls. 22, 23)

Subgenus *Ricinella* Schumacher, 1817Type: *Drupa rubusidaeus* Röding, 1798

Shell sub-ovate, solid, spire rather short; body whorl large, whorls spirally ribbed, sculptured with siphonous spiniform tubercles; interstices filled with fine scale-like plates forming raised threads; threads running spirally in close parallel association; columella with an axial fold, outer lip dentate with teeth singularly arranged, sometimes in close association, not compound; operculum subelliptical, not linear; radula typical for the genus.

This group includes besides the type species, *Ricinella speciosa* Dunker, 1867, *R. clathrata* Lamarck, 1816, and *R. clathrata miticula* Lamarck, 1822. On the basis of radular characters, the group shows a close relationship with *Drupa sensu stricto*. The shells on the other hand resemble some of the thaidids. The members of this group have the labial teeth developed as small, pearl-like teeth which may be closely crowded together as in *Drupa clathrata* or *D. speciosa*, but are never actually compound.

The interpretation of the identity of the type species of *Ricinella*, i.e. *R. purpurata* Schumacher, rests on the elucidation of the cited illustration of Favanne (1784, pl. 24, fig. 2). This figure resembles *D. rubusidaeus* Röding more so than *D. clathrata* (Lamarck). Favanne's description of the color of the aperture as being deep and vivid lilac or purple, excludes the species *D. clathrata* from consideration.

Synonymy—

- 1817 *Ricinella* Schumacher, Essai nouv. système, pp. 72, 240. Type-species by subsequent designation. Iredale, 1937: *Ricinella purpurata* Schumacher, 1817 [= *Drupa rubusidaeus* Röding, 1798].



Plate 22. Radula of *Drupa (Ricinella) rubusidaeus* Röding. Half a transverse row; Olawala, Maui, Hawaiian Ids.

Range—From the Red Sea and East Africa throughout the Indo-Pacific to Hawaii and the Tuamotu Islands.

Remarks—This solid species could only be confused with the much smaller and rarer *Drupa speciosa* (Dunker). *D. speciosa* is a higher-spined shell with no yellow coloration in the aperture; the pink coloring of the aperture is more pronounced and the denticles of the outer lip are more closely set and almost grouped.

Habitat—On algae matted reef-flats, under rocks and in tide-pools, generally on the seaward half of the reef-flat; from low tide to a depth of 10 fathoms or more, on rock, sand or coral. In the Hawaiian Islands the species has been collected attached to stony coral at a depth of 50 to 60 feet (C. S. Weaver, leg.).

Description—Shell 20 to 55 mm ($\frac{3}{4}$ to $2\frac{1}{4}$ inches) in length, solid, ovately globose, slightly ventricose, spire short, acuminate, body whorl large and with five rows of strong, sub-spiniform, siphonous tubercles. Sculpture of fine, scale like



Plate 23. *Drupa (Ricinella) rubusidaeus* Röding.

Fig. 1. Lectotype figure of *D. (R.) rubusidaeus* Röding, from Knorr, 1768, pt. 6, pl. 24, fig. 7.

Fig. 2. Holotype of *Ricinella reeveana* Crosse, from Nukuhiva, Marquesa Ids. (B.M. (NH); 48.2 x 38.8 mm—immature specimen).

plates forming ridges which run spirally in parallel association between the rows of tubercles. Aperture sub-elliptical, outer lip in adult stage dentate with 7-12 small pearl-like teeth; margin crenulated, apertural area enameled; enameled area extending over a large portion of the body whorl adjacent to the aperture. Inner lip calused with 3 or 4 plications. Siphonal canal short, deep, recurved; sutural canal conspicuous, always open. Color white-yellowish externally, margin of the aperture yellow, interior of the aperture rich pink.

The side-cusps of the rachidians of the radula are bifid to trifid and are followed by 2-3 lateral denticles, exclusive of the stronger side-cusps.

Measurements (mm)—(including spines; all specimens with a mature lip)

length	width	
53.8	48.5	Oahu, Hawaiian Ids.
48.2	38.8	Holotype of <i>reeveana</i> Crosse
41.6	38.9	Luzon Id., Philippines
34.0	28.7	Niue Id., Polynesia
28.8	25.0	Koror Id., Palau Ids.

Synonymy—

- 1742 ——— Gualtieri, Ind. test. Conchyliorum, pl. 28, fig. R (poor).
- 1758 ——— Regenfuss, Aus. Schnecken, Muscheln u.a. Schaalthiere, (1), pl. 3, fig. 32.
- 1768 ——— Knorr, Verg. Augen U. Gemüths, pt. 6, pl. 24, fig. 7 (very good).
- 1777 "*Murex hericinus*" Martini, Syst. Conchylien-Cabinet, vol. 3, p. 283, pl. 101, figs. 974, 975 (poor). [non-binomial].
- 1780 ——— Favanne, La Conchyliologie ed. 3 [of d'Argenville], pl. 24, fig. A2 (poor).
- 1784 ——— Favanne, Catalogue systematique et raisonné, p. 145 (description).
- 1791 *Murex nodus* Gmelin, Systema Naturae, ed. 13, p. 3537 (refers to Knorr, *op. cit.*, with a query) [no locality given] (non Linnaeus, 1758).
- 1798 *Drupa rubusidaeus* Röding, Museum Boltzenianum, p. 55 (refers to Martini, *op. cit.*, and Knorr, *op. cit.*) [no locality given]; 1913 Hedley, Nautilus, vol. 27, no. 7, p. 80; 1966 Weaver, Hawaiian Shell News, vol. 14, no. 14, p. 2, textfigs. 1, 2; 1969 Cernohorsky, Veliger, vol. 11, no. 4, p. 301, pl. 47, figs. 10, 10a; 1971 Wilson & Gillet, Australian Shells, p. 92, pl. 61, figs. 1, 1a.
- 1798 *Drupa fragum* Röding, Museum Boltzenianum, p. 55 (refers to *Murex nodus* Gmelin, 1791, sp. 42) [no locality given].
- 1807 *Mancinella hystrix* Link, Besch. Nat.-Samml. Univ. Rostock, 3 Abth., p. 115 (refers to Martini, *op. cit.*) [non *Murex hystrix* Linnaeus, 1758].
- 1817 *Ricinella purpurata* Schumacher, Essai nouv. système, p. 240 (refers to Favanne, *op. cit.*) [no locality given].
- 1817 *Murex hystrix* Linnaeus, Dillwyn, Desc. cat. Rec. shells, vol. 2, p. 706 (refers to Martini, Gualtieri, Regenfuss etc.) [East Indian Seas; coasts of the Friendly Islands = Tonga Ids.]; 1825 Wood, Index Testaceologicus, p. 124, pl. 26, fig. 50a (non *M. hystrix* Linnaeus, 1758).
- 1822 *Purpura hystrix* Lamarck, Hist. nat. anim. s. vertèbres, vol. 7, p. 247 (refers to Knorr, Regenfuss, Martini and Gualtieri, *op. cit.*); 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 13, pl. 2, figs. 4, 4a, b; 1846 Reeve, Conchologia Iconica, vol. 3, pl. 3, fig. 13 (non *Murex hystrix* Linnaeus, 1758).
- 1825 *Murex hippocastanum* Wood, Index Testaceologicus, p. 124, pl. 26, fig. 53a (non Linnaeus, 1758).
- 1832 *Purpura spathulifera* Blainville, Nouv. Ann. Mus. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 212, pl. 9, fig. 8 (no locality given).
- 1833 *Purpura hystrix* (sic) Lamarck, Quoy & Gaimard, Voyage L'Astrolabe, vol. 2, p. 575, pl. 39, figs. 14-16 (animal and operculum).
- 1853 *Pentadactylus hystrix* H. & A. Adams, Gen. Rec. Mollusca, vol. 1, p. 130; 1875 Troschel, Gebiss d. Schnecken, vol. 2, p. 134, pl. 13, fig. 4 (radula).
- 1862 *Ricinella reeveana* Crosse, Journal de Conchyliologie, vol. 10, p. 47, pl. 1, fig. 3 (Nouhiwa = Nukuhiva, Marquesas Ids.) [immature specimen] (non *Ricinella reeveana* C. B. Adams, 1852).
- 1880 *Ricinella hystrix* Linné, Tryon, Manual Conchology, vol. 2, p. 183, pl. 56, fig. 195; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 239.
- 1880 *Ricinella hystrix* var. *reeveana* Crosse, Tryon, *ibid.*, vol. 2, p. 183, pl. 56, fig. 196; 1933 Dautzenberg & Bouge, *ibid.*, vol. 77, p. 239 (non C. B. Adams, 1852).
- 1911 *Sistrum hystrix* Linné, Schepman, Siboga-Expeditie, vol. 49d, p. 354 (non *Murex hystrix* Linnaeus, 1758).
- 1913 *Drupa rubusidaeus* Bolten, Hedley (*pars*), The Nautilus, vol. 27, no. 7, p. 79.
- 1936 *Drupa spathulifera* (Blainville), Hirase, Coll. Jap. shells, ed. 5, p. 79, pl. 110, fig. 9; 1954 Kira, Col. illust. shells Japan, p. 47, pl. 23, fig. 4; 1967 Habe & Kotsuge, Stand. book Jap. shells color, vol. 3, p. 70, pl. 27, fig. 24; 1968 Taylor, Phil. Trans. Roy. Soc. London, ser. B, vol. 254, p. 201.
- 1938 *Drupa (Drupa) hystrix* (Linné), Adam & Leloup, Mém. Mus. Roy. d'Hist. Nat. Belgique, vol. 2, fasc. 19, p. 163.
- 1957 *Drupa rubuscaesia* Kaicher, Indo-Pacific Sea Shells (Muricea, Buccinacea), pl. 3, fig. 15 (non *D. rubuscaesia* Röding, 1798).
- 1961 *Drupa rubuscaesium* Röding, Rippingale & McMichael, Queensland and Ct. Barrier reef Shells, p. 102, pl. 13, fig. 3 (non *D. rubuscaesia* Röding, 1798).
- 1962 *Drupa rubuscaesia* (Röding), Kira, Shells West Pacific in color, vol. 1, p. 62, pl. 24, fig. 4; 1965 Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 115, pl. 13, figs. 5, 6 (radula) [non Röding, 1798].
- 1965 *Drupa speciosa* (Dunker), Wu, Bull. Inst. Zool. Acad. Sinica, vol. 4, p. 98, textfig. 30 (radula) [non *Ricinella speciosa* Dunker, 1867].
- 1967 *Drupa rubusidaeus* Röding, Orr Maes, Proc. Acad. Nat. Sci. Philadelphia, vol. 119, no. 4, p. 129.

Types—Röding's type specimen of *Drupa rubusidaeus* is lost, and we therefore select the specimen figured by Knorr on plate 24, fig. 7, as the lectotype of the species (Pl. 23, fig. 1), and designate Davao Bay, Mindanao, Philippines, as the type locality. The type specimen of *Purpura spathulifera* Blainville, is probably in the Muséum National d'Histoire Naturelle, Paris, and the holotype of *Ricinella reeveana* Crosse, is in the British Museum (Nat. Hist.) [Pl. 23, fig. 2]. The type specimen of *Ricinella purpurata* Schu-

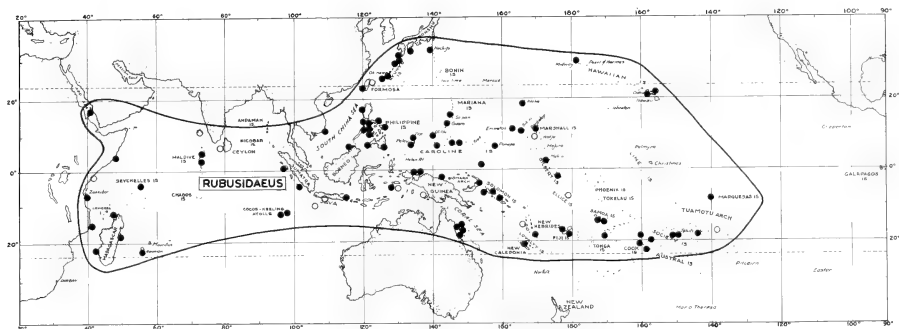


Plate 24. Geographical distribution of *Drupa (Ricinella) rubusidaeus* Röding. Open circles are literature records.

macher, could not be located in the Zoological Museum, Copenhagen (J. Knudsen, *in litt.*).

Nomenclature—This species was at first masquerading under the names *Mancinella hystrix* Link, *Murex hystrix* Dillwyn and *Purpura hystrix* Lamarck. As previously discussed, this is not *Murex hystrix* Linnaeus, 1758. Since Röding, 1798, cites 2 of the 4 references which Lamarck considered synonyms of *Purpura hystrix*, there can be no doubt regarding the identity of his species. Röding's citation to Knorr's excellent figure (designated as lectotype) of the present species, as well as Martini's figures, serves to establish the identity of *D. rubusidaeus*.

More recently Hedley (1913) confused *Purpura spathulifera* Blainville, a species which he synonymized with *Drupa rubuscaesius* Röding, *Ricinella clathrata* Lamarck, and *R. speciosa* Dunker, but which is conspecific with *D. rubusidaeus*. The specimen and its figured radula cited by Wu (1965a) as "*Drupa speciosa* (Dunker)" originated from Wan-li-tong, Taiwan, and is actually *D. rubusidaeus* Röding (Wu *in litt.*).

Records—RED SEA: (AMNH). EAST AFRICA: Gesira, Somalia (ANSP); Diani Beach, Kenya (Heinicke, 1970, p. 7); Kendwa Id., 4 mi. ESE of Dar-es-Salaam; Sinda Id., 15 mi. SSE of Dar-es-Salaam; N.W. of Magogani; Pangavini Id., 10 mi. NNE of Dar-es-Salaam, all Tanzania (all MCZ); Mozambique (USNM). SEYCHELLES ISLANDS: Beau Vallon Beach, Mahé; Cousin Id. (both ANSP). MADAGASCAR: Nosy N'Tangam, W. Nossi Bé; Grande Recife, W. of airport, Tulear; Ambodifototra (all MCZ). REUNION ISLAND: (ANSP). MALDIVES ISLANDS: Miladunmadula Atoll; Tiladummati Atoll; N. Male Atoll (all ANSP). LACCADIVE ISLANDS: (Hornell, 1922, p. 217). CEYLON: (Langdon, 1875, p. 72). VIETNAM: Cam Ranh Bay (ANSP). COCOS-KEELING ISLANDS: Klapetuju, West Id. (USNM). S. end of Home Id.; N. end of Horsburgh Id.; S. end of Direction Id. (all ANSP). CHRISTMAS ISLAND: (Tomlin, 1935, p. 79). INDONESIA: Mandi Darrah Id., N. Borneo (AMNH);

ANSP); Pulau Bai, Batu group, off Sumatra; Pulau Penju, S. Sumatra (both USNM); Bali Id.; Wasi, Ambon Id. (both FMNH); Banda Id.; Soengai Manoeibai, Iles Aroe (Adam & Leloup, 1938, p. 164); Tjilaet, Java (Altena, 1945, p. 146). PHILIPPINES: Iba, Zambales, Luzon Id.; Borongan village, E. Samar Id.; Cuyo Id., Palawan group (all ANSP); Tiliq reef, Lubang Id.; Calapan, Mindoro; Lingayan Gulf; Davao Bay, Mindanao (all AMNH); Nogas Point, Panay Id.; Cabra Id.; Silino Id.; Point Matangal, Basilan, Sulu (all USNM). FORMOSA (Taiwan): Wan-li-tong (AMNH); Karenko; Botan-wan; Ryuku-syo; Hoko (Kuroda, 1941, p. 111). RYUKYU ISLANDS: Yomitan reef, Okinawa (AMNH); Okuma, Kunigami-Gun; Bolo reef, N.W. Naka-gami-Gun (both USNM); Ishigake (MCZ); Miyako (FMNH). JAPAN: Hachijo Id., 275 mi. S. of Tokyo; Tosa, Shikoku; Kagoshima, Kyushu (all ANSP); Ominato Ise (AIM); Oshima, Osumi (Powell coll.). MARIANAS: Saipan (AMNH); Agana Bay, Guam Id. (ANSP). PALAU ISLANDS: Babelthup Id.; Angupelu Id., S.E. of Koror; Malakal Harbour, Koror; Helen Channel (all ANSP). CAROLINE ISLANDS: Kayangel; Ngargersul; S.W. of Rattakadokoru; S. of Garakayo; Ulithi; Ella; Elangalap Id.; Ifaluk Atoll; Tirakaume; Ringutor; Kapingamarangi (all ANSP); Ponape reef (AMNH). WAKE ISLAND: (BPBM). MARSHALL ISLANDS: Eniwetok Atoll; Bikini Atoll; Rongerik Atoll (all USNM); Kwajalein Atoll (Dietrich & Morris, 1953, p. 15). NEW GUINEA: Biak Id.; Schouten Ids. (USNM); 1 mi. NE of Mies Woendi, Padoado Ids. (Powell coll.); Wewak (ANSP). NEW BRITAIN: Rabaul Harbour (AMNH). AUSTRALIA: Queensland: Herald Cay, Coral Sea; Holmes reef, Coral Sea; off Cairns; Watt reef, off Townsville (all AMS); Green Id., off Cairns (AIM); several islands of the Capricorn group (AMS; AMNH). SOLOMON ISLANDS: Choiseul Bay, Choiseul Id.; Bougainville Id.; Bellona Id. (all AMNH); Fiu, Malaita Id. (Powell coll.). NEW HEBRIDES: Efate Id. (Colardeau coll.); Espiritu Santo (Solem, 1959, p. 262). NEW CALEDONIA: Touho (AMNH). GILBERT ISLANDS: Abaiang (MCZ); Kingsmill Id. (AMNH). ELLICE ISLANDS: Funafuti lagoon (AIM). FIJI ISLANDS: (AMNH; ANSP); Rat Tail Passage, Suva reef, S. Viti Levu (WOC coll.); Mamanuca group (Jennings coll.). NIUE ISLAND: (DM); Tuapa reef (AMNH; WOC coll.). SAMOA ISLANDS: reef at Satalo Id., Upolu Id.; E. side of Waiile Bay, Upolu Id. (both ANSP); Nuuli, Tutuila Id. (MCZ). COOK ISLANDS: Mauke; Aitutaki (both USNM); off Aroa Creek, S.W. Rarotonga; Koromiri Id., S.W. Rarotonga (both MCZ); Mangaia (DM). SOCIETY ISLANDS: Several localities on Tahiti and Moorea (USNM). TUA-MOTU ISLANDS: Anaa Id. (AMNH; ANSP; MCZ); Amanu (Coututirer, 1907, p. 143). MARQUESAS ISLANDS: (MCZ); Nukuhiva (BMNH). LINE ISLANDS: Fanning Id. (DMNH). HAWAIIAN ISLANDS: Midway Id.; off Waikiki, Oahu (both

(AMNH); Makaha Point, S.W. Oahu (MCZ); Olawala, Maui (AMNH).

Fossil records—KENYA: Pleistocene: raised reef, S.E. of Mombassa Id., N. of Ras Serani (Cox, 1930, p. 145). HAWAIIAN ISLANDS: Oahu Id. (Kosuge, 1969, p. 786, pl. 5, fig. 94).

Drupa speciosa (Dunker, 1867)

(Pl. 2, figs. 21, 22; Pl. 25)

Range—Tuamotu and Pitcairn Islands.

Remarks—The shell of this Polynesian species is smaller and higher-spined than *D. rubusidaeus* Röding, with a deeper pink to mauve aperture which lacks the yellow coloration found in the aperture of the larger species. Specimens labelled "Fiji Islands" are obviously based on erroneous locality indications as the species does not occur there. The record from Rarotonga, Cook Islands (ANSP) is also suspect, and has not been confirmed by recently collected, well-documented specimens.

Habitat—Unknown, but probably found on coral reefs at low tide.

Description—Shell 20 to 29 mm ($\frac{3}{4}$ to 1 $\frac{1}{4}$ inches) in length, solid, ovate, globose; spire moderately elevated, acuminate; body whorl axially ribbed with 9 ribs, crossed by 5 transverse rows of short, strong, spinose tubercles. Interstices between tubercles striated with parallel rows of small scales. Aperture subelliptical, columella posteriorly excavated, outer lip dentate with 4-7 evenly spaced small white teeth; margin crenulated. Inner lip with 3 strong lower plications and 1 subobsolete upper plication. Apertural area enameled, enameled area of the inner lip extending over a portion of the body whorl. Anterior siphonal canal short, deep; posterior siphonal canal open. Color creamy-white externally, aperture a deep mauve pink.

Radula unknown. The radular dentition figured by Wu (1965a) for this species was based on a specimen of *D. rubusidaeus* from Taiwan (Wu, *in litt.*).

Measurements (mm)—(including spines; all specimens with a mature lip)

length	width	
27.0	21.5	Tuamotu Ids.
26.9	23.2	Lectotype of <i>speciosa</i> Dunker
26.4	20.8	Raroia, Tuamotu Ids.
25.4	21.7	Vahitahi, Tuamotu Ids.
22.8	18.9	Vahitahi, Tuamotu Ids.
21.9	16.3	Vahitahi, Tuamotu Ids.
20.1	14.8	Tuamotu Ids.

Synonymy—

- 1846 *Ricinula clathrata* Lamarck, var. B., Reeve, Conchologia Iconica, vol. 3, pl. 2, fig. 9a (Anaa Id.) [non *R. clathrata* Lamarck, 1816].
 1867 *Ricinula speciosa* Dunker, Novitates Conchologicae, Abt. II, pts. 11/12, p. 100, pl. 33, figs. 7, 8; 1878 Dunker, Addenda & Corrigenda, p. 139 (Philippine Ids. = error) [non *Purpura speciosa* Valenciennes, 1832].
 1880 *Ricinula hystrix* var. *speciosa* Dunker, Tryon, Manual Conchology, vol. 2, p. 183, pl. 56, fig. 194; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 239.
 1969 *Drupa speciosa* Dunker, Cernohorsky, Veliger, vol. 11, no. 4, pp. 301, 302.

Types—Dunker described the species from 4 specimens in Hugh Cuming's collection which is now in the British Museum (Nat. Hist.). Three of the syntypes are immature examples with weak denticles on the outer lip and a superficial columellar callus. Only one specimen is reasonably mature, and this specimen is here selected as the lectotype of *Ricinula speciosa* Dunker (Pl 25, fig. 1). Even though the selected lectotype is without

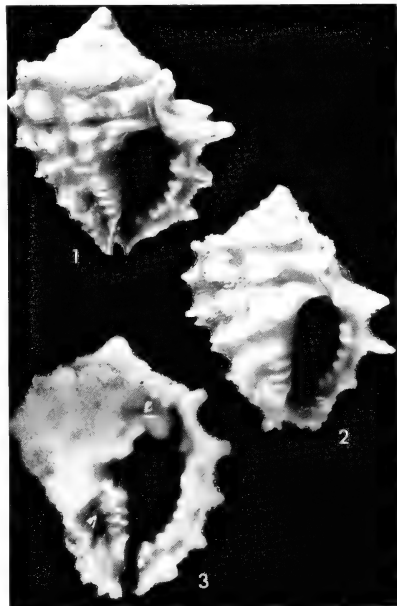


Plate 25. *Drupa (Ricinella) speciosa* (Dunker).

Fig. 1. Lectotype (B.M. (NH); 26.9 x 23.2 mm).

Fig. 2. Syntype; immature (B.M. (NH); 26.9 x 21.9 mm) [photos courtesy K. Way, B.M. (NH)].

Fig. 3. Specimen from Vahitahi, Tuamotu Ids. (USNM 613343; 22.8 x 19.0 mm).

question the *Drupa speciosa* of authors, the specimen does not compare too well with Dunker's original type-figure. Either the artist exercised his own imagination when depicting the specimen, or the originally illustrated example has gone astray. Stability of the taxon *Drupa speciosa*, however, is best served by the selection of the most mature specimen from among the 4 syntypes, which all are the *D. speciosa* of Dunker and of authors. Dunker gave the erroneous type locality as "Philippine Islands," which is here corrected to Anaa Island, Tuamotu Islands. Reeve's figure is based on a specimen in the Cuning collection from this locality.

Nomenclature—Reeve in 1846 figured this species, calling it *Ricinuia clathrata* Lamarck, variety B, and both Crosse (1862) and Dunker (1867) in describing *reeveana* and *speciosa* respectively, cite Reeve's figures in synonymy. However, *R. reeveana*, which is preoccupied (*non* C. B. Adams, 1852), has been shown to be a synonym of *D. rubusidaeus* Röding, leaving Dunker's name available for the present taxon.

Records—TUAMOTU ISLANDS: (USNM; ANSP; FMNH; AMS); Garumaoa; Mataira; Oneroa; Opakea, all Raroia Atoll (USNM); Anaa Id. (MCZ); Vahitahi (USNM); Fangatau; Makatea (Dautzenberg and Bouge, 1933, p. 239). PITCAIRN ISLAND: Oeno Island (USNM).

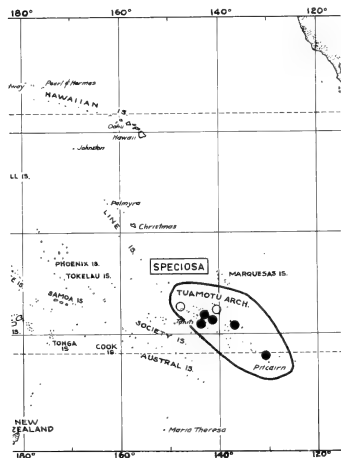


Plate 26. Geographical distribution of *Drupa (Ricinuia) speciosa* (Dunker). Open circles are literature records.

Drupa clathrata clathrata (Lamarck, 1816)

(Pl. 2, figs. 16-18; Pls. 27, 28)

Range—From Japan and the Philippines to the Marquesas and Pitcairn Islands.

Remarks—The large number of spines, rugose columella and apertural coloration serve to characterize this species. Populations occurring in the Indian Ocean are separable on shell morphology and are recognized as a subspecies, *D. clathrata miticula* (Lamarck).

Habitat—On reefs, in crevices and under coral rocks, intertidal.

Description—Shell 16 to 57 mm ($\frac{3}{4}$ to 2 $\frac{1}{4}$ inches) in length, ovate and solid, spire short; body whorl large, crossed by five rows of spiral ribs. Ribs with siphonous, spiny tubercles; tubercles higher towards the margin of the outer lip. Spiral ribs connected by low axial ribs to form shallow pockets in the interstices. Surface sculptured with fine spirally arranged scales. Aperture sub-elliptical, columella excavated posteriorly, with 4 to 5 small plications above the siphonal canal. Parietal shield thinly enameled, reflected to form an irregular callus. Sutural canal well developed as a groove turned toward the spire. Axial fold strong, extending the length of the columella and terminating as a margin of the siphonal canal. Outer lip dentate with 4 to 5 singularly arranged teeth which sometimes become united. Color brownish-white externally, margin of aperture spotted with brown, interior of aperture a light violet. Operculum typical of group.

The radula has the side-cusps of the rachidian bifid or trifid, and there are 2 to 3 deeply rooted lateral denticles, exclusive of the end-cusps.

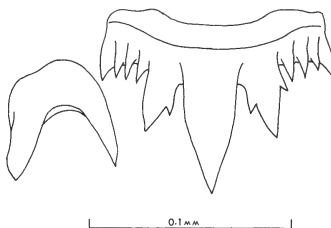


Plate 27. Radula of *Drupa (Ricinuia) clathrata clathrata* (Lamarck). Half a transverse row; Pango Point, Efate Id., New Hebrides.

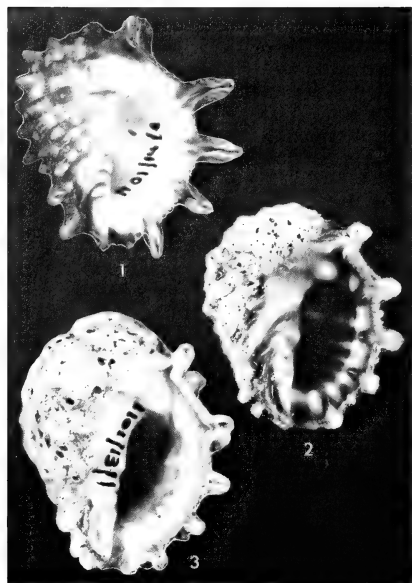


Plate 28. Figs. 1, 2. *Drupa (Ricinella) clathrata clathrata* (Lamarck); Fig. 3. *D. (R.) clathrata miticula* (Lamarck).
 Fig. 1. Holotype of *Ricinella clathrata* Lamarck (MHNG no. 1101/14/1; 30.4 x 31.2 mm).
 Fig. 2. Specimen of *Drupa (Ricinella) clathrata clathrata* (Lamarck), from Pango Point, Efate Id., New Hebrides (WOC coll.; 28.3 x 25.5 mm).
 Fig. 3. Lectotype of *Ricinula miticula* Lamarck (MHNG no. 1101/13/1; 26.3 x 21.0 mm).

Measurements (mm)—(including spines; all specimens with a mature lip)

length	width	
57.3	53.0	"South Seas"
42.8	38.2	"Central Pacific"
35.7	29.0	Suva reef, Fiji Ids.
32.2	24.6	Samar Id., Philippines
30.4	31.2	Holotype of <i>clathrata</i> Lamarck
23.1	20.0	Tacume Id., Tuamotu Ids.
21.0	18.5	Pango Pt., New Hebrides

Synonymy—

- 1816 *Ricinula clathrata* Lamarck, Tableau Encycl. Méthodique, p. 2, pl. 395, figs. 5a, b (no locality given); 1822 Lamarck, Hist. nat. anim. s. vertèbres, vol. 7, p. 231; 1846 Reeve, Conchologia Iconica, vol. 3, pl. 2, fig. 9b only (Elizabeth Id., = Tuamotu Ids.); 1859 Chenu, Manuel de Conchyliologie, vol. 1, p. 168, textfig. 816; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 237.

- 1835 *Purpura clathrata* Lamarck, Kiener (pars), Spéc. gén. icon. coq. viv., vol. 8, p. 15, pl. 3, fig. 5 only.
 1853 *Pentadactylus clathratus* Lamarck, H. & A. Adams, Gen. Rec. Mollusca, vol. 1, p. 130; 1875 Troschel, Gebiss d. Schnecken, vol. 2, p. 133, pl. 13, fig. 3 (radula).
 1880 *Ricinula hystrix* var. *clathrata* Lamarck, Tryon, Manual Conchology, vol. 2, p. 184, pl. 56, figs. 197, 198.
 1913 *Drupa rubuscaesia* Bolten, Hedley (pars), Nautilus, vol. 27, no. 7, p. 80 (non *D. rubuscaesia* Röding, 1798).
 1936 *Drupa rubuscaesia* Röding, Hirase, Coll. Jap. shells, p. 79, pl. 110, fig. 10; 1957 Kaicher, Indo-Pacific Sea Shells (Muricacea, Buccinacea), pl. 3, fig. 15 (non *D. rubuscaesia* Röding, 1798).
 1951 *Drupa rubuscaesia* Röding, Hirase & Taki, Handb. illust. shells colour, pl. 110, fig. 10; 1959 Kira, Col. illust. shells of Japan, vol. 1, p. 58, pl. 23, fig. 9 (non Röding, 1798).
 1954 *Drupa rubuscaesia* Röding, Kira, Col. Illust. shells of Japan, pl. 23, fig. 9 (non *D. rubuscaesia* Röding, 1798).
 1962 *Drupa rubsidaeus* (sic) Röding, Kira, Shells west. Pacific in colour, p. 63, pl. 24, fig. 9 (non *D. rubsidaeus* Röding, 1798).
 1965 *Drupa rubsidaeus* Röding, Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 115, pl. 13, fig. 7 (radula) [non Röding, 1798].
 1967 *Drupa (Ricinella) rubsidaeus* (Röding), Habe & Kosuge, Stand. book Jap. shells in color, vol. 3, p. 70, pl. 27, fig. 29 (non Röding, 1798).
 1969 *Drupa clathrata* (Lamarck), Cernohorsky, Veliger, vol. 11, no. 4, p. 298, pl. 47, fig. 6.

Types—The holotype of *Ricinula clathrata* Lamarck, is in the Muséum d'Histoire Naturelle, Geneva, no. 1101/14/1 (Pl. 28, fig. 1). According to Rosalie de Lamarck's marginal annotations in her father's copy of the "Histoire naturelle des animaux sans vertèbres," only a single specimen was present in Lamarck's collection at the time of description. In 1822 Lamarck gave the size of his specimen as 13½ lignes [= 30.4mm], and this dimension agrees with the larger specimen, which is considered the holotype, but not the smaller 29.7mm specimen which accompanies it. This latter specimen has probably been added at a later date. The type locality here designated is Tuamotu Islands (after Reeve, 1846), specifically Raroia Island (from which there are specimens in the ANSP).

Nomenclature—This species seems to have been confused with *Drupa rubuscaesia* Röding, and *D. rubsidaeus* Röding, by modern authors. Hedley (1913) initiated the confusion by suggesting that *Ricinula clathrata* Lamarck, *R. speciosa* Dunker and *Purpura spathulifera* Blainville, were synonyms of *Drupa rubuscaesia* Röding. Kira (1954, pl. 23, fig. 9; 1962, pl. 24, fig. 9) illustrates a specimen of *Drupa clathrata* with an immature lip and calls it in the first instance *D. rubuscaesia* Röding, and in the second instance *D. rubsidaeus* (sic) Röding. Kaicher (1957,

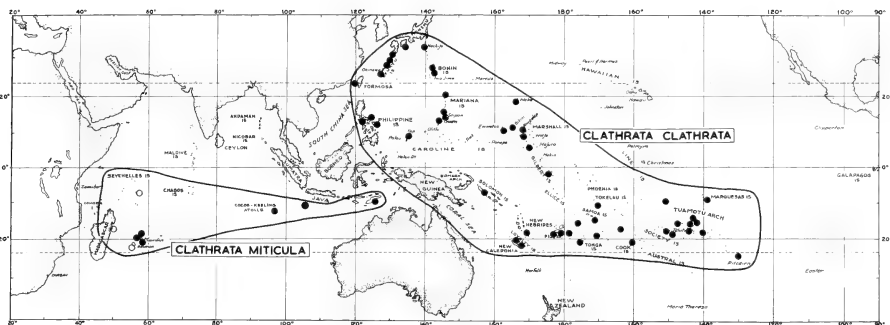


Plate 29. Geographical distribution of *Drupa* (*Ricinella*) *clathrata clathrata* (Lamarck) and its subspecies *D. (R.) clathrata miticula* (Lamarck). Open circles are literature records.

Drupa clathrata miticula (Lamarck, 1822)

(Pl. 2, figs. 19, 20; Pls. 28, 30)

Range—Madagascar to the Island of Timor in Indonesia.

Remarks—First described by Lamarck in 1822, the identity of this Indian Ocean form appears to have escaped notice for over a hundred years and in that interval has been recorded as typical *Drupa clathrata*. It lacks the brown coloration of the columella and inner and outer lips that characterize the nominate subspecies. *D. miticula* is also a smaller shell, with shorter spines. The Indian Ocean populations have a more pronounced purple color in the aperture than those of the nominate subspecies which is lavender to whitish purple. The exterior lacks the black spines of *D. morum*.

Habitat—In tide pools, basalt rock, weed and some coral, and on sand and grass, from 0 to 8 feet. In the Cocos-Keeling Islands the species was found in "strong surf on a large boulder on the northern seaward reef at Horsburgh Island" (V. Orr Maes, personal communication). On Christmas Island it was found among *Caulerpa*



Plate 30. Radula of *Drupa* (*Ricinella*) *clathrata miticula* (Lamarck). Half a transverse row; Greta Beach, Christmas Id., Indian Ocean.

Records—PHILIPPINES: Gigmoto, Catanduanes Id. (AMNH; DMNH; AIM); Borongan village, E. Samar Id. (ANSP); Marinduque Id. (USNM). FORMOSA (Taiwan): Chaiting (Janowsky coll.). RYUKYU ISLANDS: Yakushima; Onna Beach, N. of Naha, Okinawa; Bolo Point, Zampa Misaki, Okinawa (all USNM). JAPAN: Hackio Id., 275 mi S. of Tokyo; Tosa, Shikoku; Kagoshima, Kyushu (all ANSP); Oshima, Osumi (USNM). BONIN ISLANDS: Chichi Shima (ANSP); Ani Jima (USNM). MARIANAS: Lagunan Tanapag, Saipan Id.; Ngargersul Id. (both ANSP); off Leprosarium, SW Tinian Id. (MCZ); Aspurguan, Guam Id.; Ypao Point, Maug Id. (USNM). WAKE ISLAND: (AMNH). MARSHALL ISLANDS: (many atolls, see map); Eniwetok; Bikini; Rongelap; Kwajalein; Jaluit (all USNM). SOLOMON ISLANDS: Choiseul Bay, Choiseul Id. (AMNH). NEW HEBRIDES: Pango Point, Efate Id., (AIM). LOYALTY ISLANDS: Lifu (USNM; AMS). NEW CALEDONIA: Touho (AMNH). GILBERT ISLANDS: Kingsmill Id. (USNM). FIJI ISLANDS: Cuvu Beach, S. Viti Levu (AMNH); Rat Tail Passage, Suva reef, S. Viti Levu (WOC coll.); SE of Onea Driki, Lau group (USNM). TONGA ISLANDS: Ha'ateiho reef, Tongatapu; Niufo'ou (both USNM). NIUE ISLAND: (DMNH); Oneone reef; Utukio reef (both AMNH); Alofi (USNM). SAMOA ISLANDS: Tutuila Id. (ANSP); Swan's Id. (MCZ). LALOMALAVA, Savaii (DMNH). COOK ISLANDS: Bird's Id., Palmerston Atoll; North Id., Palmerston Atoll (both USNM); Avaavaroa Passage, S. Rarotonga (ANSP). SOCIETY ISLANDS: Moorea; Venus Point, Tahiti (both AMNH); Punaavai, Tahiti (ANSP). TUAMOTU ISLANDS: Tacume; Raroia (both ANSP); Anaa Id. (AMS); Makemo; Tikahau; Vahitahi; Makatea (all USNM). MARQUESAS ISLANDS: Atuona Bay, Hiva-Oa Id. (ANSP). PITCAIRN ISLAND: (AMNH). LINE ISLANDS: Caroline Id. (ANSP); Jarvis (DMNH).

mats and in rock and tide-pools (leg. A. Slack-Smith and A. Patterson).

Description—Shell 16 to 38 mm ($\frac{3}{4}$ to $1\frac{1}{2}$ inches) in length, ovate, globose, spire short, acuminate. Body whorl large with six transverse rows of short tubercles. Interstices between tubercles striated with four to six rows of closely spaced granules. Aperture moderately wide, oval, over three-quarter of shell length. Outer lip crenulated between tubercles, inner margin dentate with six small white teeth from which six conspicuous white raised lines run into the aperture. Inner lip enameled with three to four plait-like ridges projecting into the aperture. Columella excavated posteriorly. Posterior siphonal canal open, obliquely curved toward the apex. Color pale brown on the exterior, interior of aperture purple.

In the radula examined, one of the side-cusps of the rachidian was trifid while the other one was simple; there were 2 lateral denticles apart from the end-cusps.

Measurements (mm)—(including spines; all specimens with a mature lip).

length	width	
38.0	31.3	Christmas Id., Indian Ocean
34.3	28.0	S. Mahébourg, Mauritius
32.5	26.0	S. Mahébourg, Mauritius
26.3	21.0	Lectotype of <i>miticula</i> Lamarck
17.0	13.8	Christmas Id., Indian Ocean
16.5	14.5	Souillac, Mauritius

Synonymy—

- 1822 *Ricinula miticula* Lamarck, Hist. Nat. anim. s. vertébrés, vol. 7, p. 231 (no locality given); 1832 Blainville, Nouv. Ann. Mus. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 211; 1844 Deshayes & Milne-Edwards, Hist. nat. anim. s. vertébrés, ed. 2, vol. 10, p. 48 (refers to Kiener, fig. 5, junior = fig. 5a, 5a).
 1835 *Purpura clathrata* Lamarck, Kiener (*pars*), Spéc. gén. icon. coq. viv., vol. 8, p. 15, pl. 3, figs. 5a, 5a (*non Ricinula clathrata* Lamarck, 1816).
 1968 *Drupa clathrata* Lamarck, Taylor, Phil. Trans. Roy. Soc. London, ser. B, vol. 254, p. 201 (*non Ricinula clathrata* Lamarck, 1816).

Types—Two syntypes of *Ricinula miticula* are in the Muséum d'Histoire Naturelle, Geneva. The slightly larger specimen, length 26.3 mm (Pl. 28, fig. 3), no. 1101/13/1, is here selected as the lectotype of *R. miticula*. No type locality was given, and Mahébourg, Mauritius, is here designated as the type locality (specimens in AMNH).

Nomenclature—Kiener (1835) regarded *Ricinula miticula* of Lamarck to be a juvenile of *R. clathrata*, but his figures are typical *R. clathrata miticula*.

Records—(Specimens): MAURITIUS: Gris Gris, 1 mi. ESE of Souillac; Vacoas Point, 3 mi. S. of Mahébourg; Point Pimente, N. side Arsenal Bay; Pointe Fayette; Caves Point (all ANSP); Mahébourg (AMNH); near Port Louis (MCZ). COCOS-KEELING ISLANDS: N. end of Horsburgh Id (ANSP). CHRISTMAS ISLAND: Lily Beach; Greta Beach; Dolly Beach (all WAM). INDONESIA: Timor (AMS).

Records—(Literature—identified as "*clathrata*"): SEYCHELLES ISLANDS: Coetivy Id. (Melvill, 1909, p. 104); Mahé (Taylor, 1968, p. 201), MADAGASCAR: (Dautzenberg, 1923, p. 38). MAURITIUS: (Viader, 1937, p. 32). REUNION ISLAND: (Deshayes, 1863, p. 115).

Drupa grossularia Röding, 1798

(Pl. 2, figs. 23, 24; Pls. 31, 32)

Range—From the Cocos-Keeling Islands in the Indian Ocean to West Australia and throughout the Pacific to Hawaii and the Marquesas Islands.

Remarks—This is a very distinctive species with the large digitate processes and solid yellow aperture distinguishing it from all other members of the genus except *Drupa lobata* (Blainville), a dark brown apertured form inhabiting the Indian Ocean.

Habitat—Lives clinging to rocks exposed at low tide or in a few feet of water on windward rather than leeward reefs. Demond (1957) records a specimen taken alive at a depth of 32-38 feet in a lagoon west of Saipan.

Description—Shell 18 to 33 mm ($\frac{3}{4}$ to 1 $\frac{1}{4}$ inches) in length, ovate, spire very short, body whorl large. Whorls spirally ribbed with low rounded nodules most common; nodules often as siphon-

Subgenus Drupina Dall, 1923**Type:** *Drupa grossularia* Röding, 1798

Shell sub-ovate, strong, heavy, flattened dorso-ventrally, spire short; whorls ribbed spirally with inconspicuous nodules, surface sculptured with minute imbricated scales; columella doubly plicated axially, outer lip with two well developed marginal processes. Operculum typical for genus. Radula with a broad but low rachidian which has from 13-18 cusps; the central cusp may be large or small and the 2 flanking side-cusps are tridentate and usually smaller than the central cusp. The lateral teeth are small and slender, with a smaller and more rounded base than in *Drupa sensu stricto*.

The 2 members of this subgenus have a portion of the outer lip expanded as two conspicuous lobate processes. The process develops as the individual reaches maturity and thus is not laid down and re-absorbed by the mantle as the shell grows; instead the processes are thickened, extended and often bifurcated. Both species of the subgenus *Drupina* are Indo-Pacific in distribution.

Synonymy—

1923 *Drupina* Dall, Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 75, p. 303. Type-species by original designation: *Ricinuia digitata* Lamarck, 1816 [= *Drupa grossularia* Röding, 1798].

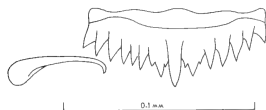


Plate 31. Radula of *Drupa (Drupina) grossularia* Röding. Half a transverse row; Fiji Islands.

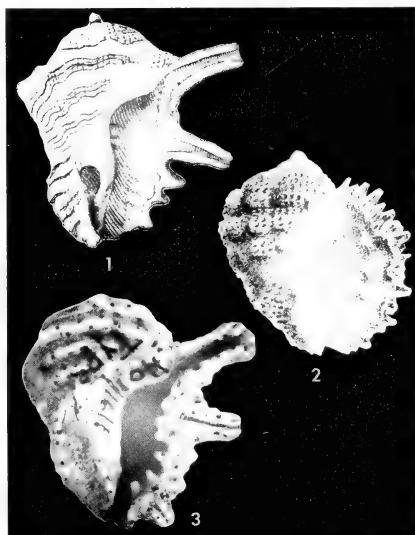


Plate 32. *Drupa (Drupina) grossularia* Röding.

Fig. 1. Lectotype figure of *Drupa grossularia* Röding, from Martini, 1777, Syst. Conchylien-Cabinet, vol. 3, pl. 102, fig. 978.

Fig. 2. Type figure of *Purpura laurentiana* Petit de la Saussaye, from Journal de Conchyliologie, 1850, vol. 1, pl. 13, fig. 2; Pacific Ocean (20.0 x 16.0 mm—juvenile specimen).

Fig. 3. Lectotype figure of *Ricinuia digitata* Lamarck (MHNC no. 1101/16/1; 22.4 x 22.0 mm).

ous tubercles near the margin of the aperture. Sculpture of crisp, well-defined scales; detail of sculpture retained only in well preserved individuals. Aperture in adult stage, linear, constricted by 5 or 6 singularly arranged, close-set teeth projecting from the outer lip, and a columellar callus with from 2-5 inconspicuous plications. Columella doubly folded axially. Aperture of juvenile specimens expanded. In adults, siphonous, digitate processes extend from the first and second ribs of the body whorl. The processes tend to bifurcate at maturity; canal of the upper process canaliculate, lower canal generally sealed in the adult stage. Exterior of shell white or cream, aperture yellow to orange, denticles of outer lip white, columellar plications faintly whitish. Operculum typical for the genus, dark orange-brown in color.

The radula is of a considerably modified drupine type and has been described in the subgeneric diagnosis. The size and length of the central tooth and accessory lateral denticles are quite variable.

Measurements (mm)—(including digitations; all specimens with a mature lip).

length	width	
32.7	33.6	Limu, Niue Island
32.0	30.9	S. Luzon Id., Philippines
23.2	22.2	Kavieng, New Ireland
22.4	22.0	Lectotype of <i>Digitata</i> Lamarck
18.7	18.3	Bougainville, Solomon Ids.

Synonymy—

- 1685 ——— Lister, Hist. Syn. Meth. Conchyliorum pl. 804, fig. 12.
 1758 ——— Seba, Locupl. rer. nat. thes. descriptio, vol. 3, pl. 60, fig. 48.
 1777 "*Murex Morum globosum*" Martini, Syst. Conchylien-Cabinet, vol. 3, p. 280, pl. 102, figs. 978, 979 (non binomial).
 1791 *Murex neritoides* Gmelin (*pars*), Systema Naturae, ed. 13, p. 3537 (refers to Seba, *op. cit.*, Lister, *op. cit.*, and Martini, figs. 978, 979 only) [non Linnaeus, 1767].
 1798 *Drupa grossularia* Röding, Museum Boltinianum, p. 55 (refers to Martini, *op. cit.*) [no locality given]; 1913 Hedley, Nautilus, vol. 27, no. 7, p. 80; 1957 Kaicher, Indo Pacific Sea Shells (Muricea, Buccinacea), pl. 4, fig. 4; 1970 Salvat, Cahiers du Pacifique, no. 14, p. 46.
 1816 *Ricnula digitata* Lamarck, Tableau Encyclopédique Méthodique, p. 2, pl. 395, figs. 7a, b (no locality given); 1822 Lamarck, Hist. nat. anim. s. vertèbres, vol. 7, p. 232; 1827 Crouch, Illust. Introduct. Lamarck's Conchology, p. 36, pl. 18, fig. 8; 1842 Reeve (*pars*), Conchologia Systematica, vol. 2, p. 215, pl. 256, fig. 3 only; 1846 Reeve, Conchologia Iconica, vol. 3, pl. 1, fig. 2a (Lord Hood Id. = S. Maratea Id.); 1859 Chemu, Manuel de Conchyliologie, vol. 1, p. 168, text fig. 815; 1880 Tryon, Manual of Conchology, vol. 2, p. 185, pl. 56, fig. 191 and pl. 57, fig. 203; 1933 Dautzenberg & Bouge, Journal de Conchyliologie, vol. 77, p. 237.

- 1842 *Purpura monstrosa* Lesson, Rev. Zool. Cuvierienne, vol. 5, App. p. 103 [Gambier Islands].
 1823 *Murex fimbriatus* Mawe. Linn. Syst. Conchology, p. 131, pl. 26, fig. 4 (non Brocchi, 1814; nec Lamarck, 1822).
 1825 *Murex ricinus* Wood, Index Testaceologicus, pl. 26, fig. 51a (non Linnaeus, 1758).
 1832 *Purpura digitata* Lamarck, Blainville, Nouv. Ann. Mus. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 210; 1833 Quoy & Gaimard, Voyage L'Astrolabe, vol. 2, p. 578, pl. 39, figs. 20-22 (shell, animal and operculum) [Carteret Harbour, New Ireland]; 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 16, pl. 3, figs. 6, 6a.
 1850 *Purpura laurentiana* Petit de la Saussaye, Journal de Conchyliologie, vol. 1, no. 4, p. 403, pl. 13, fig. 2 (Pacific Ocean) [juvenile specimen].
 1853 *Pentadactylus grossularius* Bolten, H. & A. Adams, Gen. Rec. Mollusca, ser. 3, vol. 1, p. 129 and vol. 3, pl. 13, fig. 6c; 1875 Tröschel, Gebiss d. Schnecken, vol. 2, p. 133, pl. 13, fig. 1 (radula).
 1880 *Ricnula hystrix* var. *laurentiana* Petit, Tryon, Manual of Conchology, vol. 2, p. 184, pl. 56, fig. 192 (juvenile specimen).
 1908 *Pentadactylus* (*Pentadactylus*) *digitatus* Lamarck, Horst & Schepman, Cat. Syst. Moll. Mus. Hist. Nat. Pays-Bas, vol. 13, p. 157.
 1929 *Drupina grossularia* Röding, Iredale, Mem. Queensland Museum, vol. 9, pt. 3, p. 290; 1961 Rippington & McMichael, Queensl. & Gt. Barrier reef Shells, p. 102, pl. 13, fig. 2; 1962 Kira, Shells west. Pacific in color, p. 62, pl. 24, fig. 3; 1965 Arakawa, Venus: Jap. Journ. Malacology, vol. 24, no. 2, p. 116, pl. 13, figs. 8-10 (radula); 1969 Cernohorsky, Veliger, vol. 11, no. 4, p. 303, pl. 48, fig. 11 (shell), text fig. 7 (radula); 1971 Wilson & Gillett, Australian Shells, p. 92, pl. 61, figs. 5, 5a; 1971 Kay, Pacific Science, vol. 25, pp. 263, 275.
 1952 *Sistrum digitatum* Lamarck, Morris, Field Guide to shells Pacific coast and Hawaii, p. 187, col. pl. 5, fig. 5; pl. 39, fig. 3.
 1965 *Drupina grossularia* (*sic*) (Röding), Wu, Bull. Inst. Zool. Acad. Sinica, vol. 4, p. 99, text figs. 20, 21 (radula); 1967 Habe & Kosuge, Stand. Book Jap. shells in color, vol. 3, p. 70, pl. 27, fig. 22 (invalid emendation).
 1968 *Drupa* (*Drupina*) *grossularia* Röding, Orr Maes, Proceedings of the Academy of Natural Sciences of Philadelphia, vol. 119, no. 4, p. 130.

Types—The holotype of *Drupa grossularia* is no longer traceable and the specimen figured by Martini on plate 102, figs. 978, 979 (Pl. 32, fig. 1) which was cited by Röding, is here designated as the lectotype of the species. Two syntypes of *Ricnula digitata* Lamarck, are in the Muséum d'Histoire Naturelle, Geneva, and the 22.4mm long specimen, no. 1101/16/1, which most closely corresponds to Lamarck's cited dimensions, is here selected as the lectotype (Pl. 32, fig. 3). The holotype of *Purpura laurentiana* Petit de la Saussaye, is in the Muséum National d'Histoire Naturelle, Paris (Journ. de Conchyliologie coll.). No type locality was given by Röding for *D. grossularia*, and the earliest record of Carteret Harbour, New Ireland, by Quoy & Gaimard,

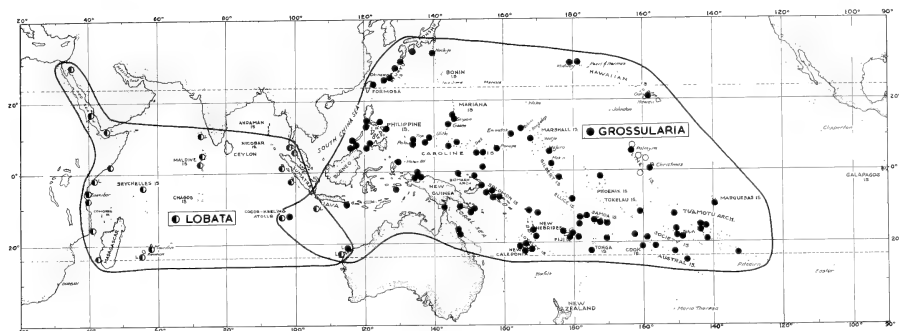


Plate 33. Geographical distribution of the species *Drupa* (*Drupina*) *grossularia* Röding, in the Pacific and East Indian Oceans (full circles) and *D. (D.) lobata* (Blainville) in the Indian Ocean (half-open circles).

1833, is here designated as the type locality, as well as for *Purpura digitata* Lamarck. Two syntypes of *Purpura monstrosa* Lesson, which are said to be "typical" examples of *D. grossularia*, are in the Muséum National d'Histoire Naturelle, Paris (*teste* G. Richard).

Nomenclature—There can be no doubt as to Röding's concept of *Drupa grossularia*, as he, Schumacher and Lamarck, all cite identical figures in Martini, 1777. Petit's *Purpura laurentiana* is a young specimen in which the mature lip has not started to form and has the whorls covered with a foreign growth (Pl. 32, fig. 2). A similar juvenile is illustrated on Pl. 2, fig. 24.

Records—COCOS-KEELING ISLANDS: S. end of Home Id. (ANSP). INDONESIA: Marudu Bay, N. Borneo (ANSP); Malawali Channel, N. Borneo (AMNH; USNM); Bali: Morotai Id. (both AMS); Oong Bay, Mandidi Id., Moluccas (MCZ); Pulau Pombo, Wasi, Ambon Id. (FMNH). PHILIPPINES: Recorded from many localities throughout the Archipelago: Luzon; Mindoro; Catanduanes; Busanga; Balabac; Sulu Archipelago (AMNH; ANSP; MCZ; USNM); Borongan village, E. Samar Id. (AIM). FORMOSA (Taiwan): Now Wow (USNM). RYUKYU ISLANDS: Sobu; Kadena; Mekaniko; Onna reefs; Bolo Point, all Okinawa (all AMNH); Miyako (FMNH). JAPAN: Hachijo Id., 275 mi. S. of Tokyo; Tosa, Shikoku; Oshima, Osumi (all ANSP). MARIANAS: Lagunan Tanapag, Saipan; Agat Bay, Guam (both ANSP); Tinian Id. (MCZ). PALAU ISLANDS: Helen reef, Koror; Babelthup (both ANSP). CAROLINE ISLANDS: S. of Carabayo; Kayangel; Rattakadokoru; Ngaruang; Ngangersul; Ponape; Yap (all ANSP); Elato Atoll; Lamotrek Atoll; Satawal Atoll; Kapingamarangi (all USNM); Lukunor (AMNH). MARSHALL ISLANDS: Eniwetok Atoll; Bikini Atoll; Kwajalein Atoll (all USNM); Armo Atoll (AMNH). ADMIRALTY ISLANDS: Manus Id. (DM). NEW BRITAIN: Rabaul (AMNH; USNM). NEW IRELAND: Kavieng (AMNH). NEW GUINEA: Aori Id.; Geelvink Bay; SW Biak, Schouten Ids.; Woori Bay, Japan Id.; 1 mi. NE Mieses Woendi, Paddaio Ids. (all ANSP); Samarai, Papua; Port Moresby, Papua (both

AMNH); Milne Bay, Papua (USNM). AUSTRALIA: Torres Strait (Shirley, 1912, p. 102); Queensland: Michaelmas Cay, off Cairns; Bramble Bay, off Lucinda (both AMS); West Australia: Barrow Id. (Wilson & Gillet, 1971, p. 92). SOLOMON ISLANDS: Vanikoro Id., Santa Cruz group; Reef Id., Santa Cruz group (both AMS); Kieta, Bougainville Id.; Lutee, Choiseul Id.; Ataa, N. Malaita Id. (all AMNH); Ugi Id., Shortland group (USNM); Ticopia Id., (AIM); NEW HEBRIDES: Meli Id., SW Efate Id.; Pango Point, Efate Id. (both AIM); Pentecost Id. (Powell coll.). LOYALTY ISLANDS: Lifu (AMS). NEW CALEDONIA: Touho (AMNH); Bourail; 7 mi. SW Gatope Id., Voh (both ANSP). FIJI ISLANDS: 3 mi. NE Tunulua, Vanua Levu (MCZ); Suva Harbour, S. Viti Levu; Ogea Levu, Ogea, Lau group (both USNM); Wadigi Id., Mamanuca group (WOC coll.). GILBERT ISLANDS: Ahaing (MCZ); Onotua Atoll, Kingsmill Ids. (USNM). ELLICE ISLANDS: Funafuti (AMS; AIM). WALLIS & FUTUNA: Nukuhifala, Wallis Id.; W. coast of Uvea, Wallis Ids.; E. side of Faioa, Wallis Ids. (all USNM); Anse de Sigave, Hoorn Id., Futuna Ids. (USNM). SAMOA ISLANDS: Asau Harbour, Savaii (USNM); Vailele Bay, Upolu Id. (ANSP); Satalo Id., Upolu Id. (AIM); Apia, Upolu Id. (Powell coll.); Pago Pago, Tutuila Id. (AMNH; MCZ). TONGA ISLANDS: Ha'ateiho, Tongatapu (USNM). NIUE ISLAND: Limu (AMNH); Alofi (USNM). PHOENIX ISLANDS: Enderbury Id. (USNM). COOK ISLANDS: Akamaru, Manihiki Atoll (ANSP); Bird's Id. and Tom's Id., Palmerston Atoll; Motu Akaia, Aitutaki (all USNM); Mauke (ANSP); several localities on Rarotonga (MCZ; USNM; AIM). AUSTRAL ISLANDS: Rurutu; Raivavae (both USNM). SOCIETY ISLANDS: N. of Fare, Huahine; Fareline, NW Moorea; Papeete, Tahiti (all USNM). TUA-MOTU ISLANDS: Raroia Id.; Lord Hood Id. [= S. Marutea Id.] (both AMNH); Makemo Id.; Toau Atoll (both ANSP); Nengonengo Id. (USNM). GAMBIE ISLANDS: Mangareva Id. (USNM). MARQUESA ISLANDS: (USNM; ANSP). LINE ISLANDS: Palmyra Id.; Flint Id.; Christmas Id. (all ANSP); Fanning Id.; Kingman reef; Washington Id.; Jarvis Id. (all Kay, 1971, p. 275). HAWAIIAN ISLANDS: Kure Id.; Midway Id. (both USNM; Makua, Oahu (Adams, 1967, p. 4).

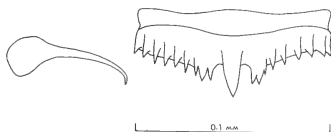


Plate 34. Radula of *Drupa* (*Drupina*) *lobata* (Blainville). Half a transverse row; Veeckens Bay, S. Pagi Id., Indonesia.

***Drupa lobata* (Blainville, 1832)**

(Pl. 2, figs. 25, 26; Pls. 34, 35)

Range—From the Red Sea and East Africa through the Indian Ocean to Thailand, Sumatra and West Australia.

Remarks—Despite its closeness to *Drupa grossularia*, the present chocolate-mouthed species seems to be a distinct form which replaces the yellow-mouthed species in the Red Sea and Indian Ocean. Their ranges are known to overlap in the Cocos-Keeling Islands where the two forms were collected at Home Island and no intermediates were found (Ostheimer and Orr Maes *leg.*), and along the coast of West Australia (specimens in West Australian Museum).

Habitat—On intertidal wave-swept reefs. In the Cocos-Keeling Islands it was found on the tops and sides of rocks near shore on the seaward reefs, and on the seaward ends of passes (Orr Maes, personal communication).

Description—Shell 18 to 32 mm ($\frac{3}{4}$ to $1\frac{1}{4}$ inches) in length, very similar to *Drupa grossularia* Röding, but differing in having a chocolate-brown aperture, a brownish dorsum, and in having a wider, more lobate digitate process extending from the first rib on the body whorl. This process shows no tendency to bifurcate as it does in *D. grossularia*, and the canal remains open in the adult.

The radula is similar to that of *D. grossularia*; the side-cusps of the rachidian are short, broad and trifid, and are followed by 6 moderately deeply rooted lateral denticles.

Measurements (mm)—(including digitations; all specimens with a mature lip)

length	width	
33.2	33.0	Mauritius
28.6	27.8	Kiwengwa, Zanzibar
26.5	26.3	Syntype of <i>dactyloides</i> Schumacher
26.2	27.5	Eilat, Gulf of Aqaba
18.5	17.5	Zanzibar

Synonymy—

- 1817 *Ricinella dactyloides* Schumacher, Essai nouv. système, p. 241 (refers to Martini, 1777, vol. 3, pl. 102, figs. 978, 979 = *Drupa grossularia* Röding) [no locality given] (*nomen oblitum*).
 1823 *Ricinula digitata* Lamarck, Sowerby, Gen. Rec. foss. shells, pt. 18, pl. 235, figs. 3, 4 (no locality given) [non Lamarck, 1816].

- 1832 *Purpura lobata* Blainville, Nouv. Ann. Mus. d'Hist. Nat. Paris, ser. 3, vol. 1, p. 210, pl. 9, fig. 7 (no locality given); 1835 Kiener, Spéc. gén. icon. coq. viv., vol. 8, p. 18, pl. 3, fig. 7.
 1842 *Ricinula digitata* var. *Lamarck*, Reeve (*pars*), Conchologia Systematica, vol. 2, p. 215, pl. 256, fig. 4 only (non Lamarck, 1816).
 1844 *Ricinula digitata* var. *fusca* "Sowerby," Deshayes & Milne-Edwards, Hist. Nat. anim. s. vertèbres, ed. 2, vol. 10, p. 53 (no locality given) [published in synonymy of *R. lobata* Blainville—refers to Sowerby, 1823, pl. 235, fig. 4] (non *R. fusca* Küster, 1862).
 1846 *Ricinula digitata* var. *B. Reeve*, Conchologia Iconica, vol. 3, pl. 1, fig. 2b (Seychelles Ids.) [non Lamarck, 1816].
 1880 *Ricinula digitata* var. *lobata* Blainville, Tryon, Manual Conchology, vol. 2, p. 185, pl. 57, fig. 205.
 1896 *Ricinula lobatus* Blainville, Shopland, Journ. Bombay Soc. Nat. Hist., vol. 10, p. 220.
 1903 *Sistrum digitatum* (var. *lobata*) E. A. Smith in Gardiner, Fauna & Geog. Maldives & Laccadive Archipelago, p. 609.
 1919 *Drupa digitata* var. *lobata* Blainville, Cooke, Proc. Malac. Soc. London, vol. 13, pt. 4, p. 101 (description of radula); 1937 Viader, Mauritius Inst. Bull., vol. 1, pt. 2, p. 32.
 1913 *Ricinula lobata* Blainville, Hedley, Nautilus, vol. 27, no. 7, pp. 79, 80; 1922 Hornell, Madras Fish. Dept. Bull., no. 6, p. 217.
 1950 *Drupa (Drupina) grossularia lobata* Blainville, Abbott, Bull. Raffles Museum, vol. 22, p. 80.
 1956 *Drupa (Drupina) lobata* (Blainville), Franc, Ann. L'Inst. Océanog. Monaco, N.S. 32, p. 37 (Ile Abulat, Red Sea); 1967 Orr Maes, Proc. Acad. Nat. Sci. Philadelphia, vol. 119, no. 4, p. 130, pl. 11, fig. E.
 1961 *Drupa lobata* Spry, Tanganyika Soc. Notes & Record, no. 56, p. 21, pl. 7, fig. 142.
 1969 *Drupina lobata* (Blainville), Cernohorsky, Veliger, vol. 11, no. 4, p. 303 1970 Heimicke, Hawaiian Shell News, vol. 18, no. 7, p. 6, text fig.; 1971 Wilson & Gillett, Australian Shells, p. 92, pl. 61, fig. 4 (Pt. Cloates, West Australia).

Types—The type specimen of *Purpura lobata* Blainville, is presumably in the Muséum National d'Histoire Naturelle, Paris. Five probable syntypes of *Ricinella dactyloides* Schumacher, are in the Zoological Museum, Copenhagen. Four of these specimens have the letters "Sp" marked either in the aperture or on the dorsum, and these originated from the Spengler collection. One specimen is marked "Sch" [= Schumacher] inside the aperture (Pl. 35, fig. 1). The type locality of *D. lobata* is here designated as Mogadiscio, Somalia.

Nomenclature—When Schumacher described *Ricinella dactyloides*, his diagnosis consisted of only the three words "labio externo digitato"; for an illustration he referred to Martini's figures 978, 979, which represent *Drupa grossularia* Röding. However, the extant and probable syntypes of *Ricinella dactyloides* are referable to the species *Drupa lobata* (Blainville), and Schumacher's *taxon* would in effect have 15 years



Plate 35. *Drupa (Drupina) lobata* (Blainville).

Fig. 1. Probable syntype of *Ricinella dactyloides* Schumacher; marked: "Sch[umacher]" inside aperture (ZMC; 26.5 x 26.3 mm).

Fig. 2. Probable syntype of *R. dactyloides* Schumacher; marked: "Sp[engler]" inside aperture (ZMC; 26.8 x 25.8 mm).

priority over Blainville's. Since Schumacher's name has not once been applied to a taxon as the valid name during the last 50 years, it is considered to be an unused senior synonym. The taxon *Purpura lobata* Blainville, however, has been in general current use during the preceding

fifty years, and has been used by 5 different authors in 10 publications (see Declaration 43 of the ICZN; Bull. Zool. Nomencl., vol. 27, pts. 3/4, p. 135).

Hedley (1913) suggested that the name *fusca* Deshayes & Milne-Edwards, 1844, be applied to the present species on the mistaken belief that Blainville had proposed *Purpura lobata* for the yellow-apertured *Drupa digitata* (Lamarck) [= *D. grossularia* Röding]. Blainville (1832, p. 210) clearly states: "couleur d'un brun-marron en dehors et à la circonférence de l'ouverture, blanche en dedans"; the type-figure given by Blainville (1832, pl. 9, fig. 7) is also an excellent representation of the dark brown apertured form, despite the lack of cited locality.

Records—RED SEA: Eilat, Gulf of Aqaba, Israel (A. Hadar; K. Haim; AMNH; DMNH); Ile Abulat (Franc, 1956, p. 37); Jidda, Saudi Arabia (DMNH). GULF OF ADEN: Aden (Shopland, 1896, p. 220). EAST AFRICA: 9 mi. N. of Mogadiscio, Somalia (ANSP); at 19 km marker, N. of Mogadiscio, Somalia (AMNH); Diani Beach, Kenya (Heinicke, 1970, p. 7); 15 mi. SSE of Dar-es-Salaam, Tanzania; 4 mi. ESE of Dar-es-Salaam, Tanzania (both MCZ); Mozambique City, Mozambique (ANSP). ZANZIBAR: Pange Id.; Kivengwa; Mangapivani (all ANSP). SEYCHELLES: Beau Vallon Beach, Mahé (ANSP). MADAGASCAR: Grande Recife, W. end of ship pier, Tuléar; Grande Recife, W. of airport, Tuléar (both MCZ). REUNION: (Deshayes, 1863, p. 115). MAURITIUS: NW side of Tamarin Bay (ANSP). MALDIVÉ ISLANDS: Imma Id., N. Male Atoll; Fodiffolu Atoll; Ari Atoll (all ANSP). LACCADIVE ISLANDS: (Hornell, 1922, p. 217). THAILAND: Goh Phi Phi; Goh Huyong, Similan Ids. (both USNM). COCOS-KEELING ISLANDS: N. tip West Id.; S. end of Direction Id.; S. end Home Id. (all ANSP). CHRISTMAS ISLAND: (Tomlin, 1935, p. 79). INDONESIA: Pulau Siburu, N. of Sipora, S.W. Sumatra; Pulau Bai, Batu group, off Sumatra; W. shore Veeckens Bay, S. Pagi Id. (all USNM). WEST AUSTRALIA: W. of Ningaloo homestead, Pt. Cloates, 22°42'S and 113°39'E (WAM).

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fimbriatus Mawe, 36	14-860	rhombiformis K. Martin, 5	14-805
fragum, Röding, 28	14-842	Ricinella Schumacher, 27	14-841
fusca Deshayes & Edwards, 38	14-862	Ricinula Lamarck, 14	14-818
glans Röding, 9	14-809	Ricinulus Demarest, 14	14-818
globosa Mörch, 16	14-820	ricinus Linnaeus, 19	14-823
globosum Martini, 16	14-820	rubuscaesius Röding, 20	14-824
grossularia Röding, 35	14-859	rubuscestus Dall, 20	14-824
hadari Emerson & Cernohorsky, 23	14-827	rubusidaeus Röding, 27	14-841
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hystrix Linnaeus, 20	14-824	styriaca Stur, 5	14-805
hystrix auctt., 28	14-842	Thaidinae, 13	14-817
iodostoma Lesson, 18	14-822	trapa Röding, 9	14-809
jodostoma Boettger, 19	14-823	tribulus Röding, 20	14-824
		uva Röding, 9	14-809
		violacea Schumacher, 16	14-820
		vitiensis Pilsbry in P. & B., 9	14-809
		walkerae Pilsbry & Bryan, 9	14-809

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By Robert Robertson. (Put in Binder 1, just after the guide tab "Phasianellidae")
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THE GENUS *GABRIELONA* (PHASIANELLIDAE) IN THE INDO-PACIFIC AND WEST INDIES

by ROBERT ROBERTSON

Pilsbry Chair of Malacology
The Academy of Natural Sciences of Philadelphia

This is the first part to be published of a monograph on the systematics of all the Indo-Pacific Phasianellidae. The other parts will comprise a general introduction, methods, a bibliography, index, and treatments of the genera *Phasianella* and *Tricolia* (including the subgenus *Hiloe* Pilsbry). Conventional approaches to the systematics of these groups, i.e. studies of shells and radulae, have yielded inconclusive results on how species should be categorized, and further biological studies are planned on them. The data on *Gabrielona* systematics are published in the meantime because they involve fewer unresolved problems and because there are new taxa (*G. pisinna*,

G. raunana goubini and *G. sulcifera*). Biological data relevant to systematics are unlikely to be obtained for this rarely collected genus.

Small, low-spired *Tricolia* specimens, which are far more common than *Gabrielona*, have been mistaken for *Gabrielona*. The generic characters detailed in this paper should help to dispel such misidentifications in the future. *Gabrielona* is distantly related to the other two genera grouped in the Phasianellidae.

Genus *Gabrielona* Iredale, 1917

Type-species: *Phasianella nepeanensis*
Gatliff and Gabriel, 1908

Chief distinguishing characters—The shells are small (*G. hadra*, the largest known species, can be 3.3 mm. long), with globose outlines and low

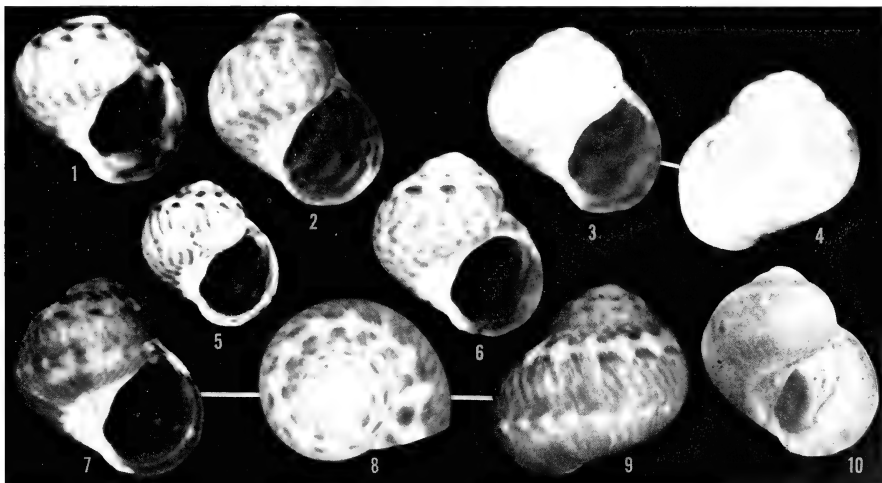


Plate 36. *Gabrielona nepeanensis* (Gatliff and Gabriel). Figs. 1-2, 5, 7-9. South Australia. Figs. 3-4, 6, 10. Victoria, Australia.

Fig. 10. Holotype. Fig. 1, x30; Figs. 2-10, x20.

spires. Sculpture, if present, is most prominent on the early whorls. Colors are pinks, reds, or browns, and white. Inside the aperture there is a spiral palatal sulcus which, if high in the aperture, is positioned beneath a spiral, subsutural feature of the color pattern on the external surface. All the species but *G. raunana* have from one to three apertural denticles. All the species are umbilicate, with an umbilical channel.

From shells of other Phasianellidae of generally similar shape and size, *Gabrielona* is most readily recognized by its operculum which, externally, has a pronounced marginal ridge and a concave central region. The other two genera have opercula that, externally, are convex. When fully withdrawn into the aperture, the operculum of *Gabrielona* fits shallowly against an axial ridge (or series of faint ridges); the opercula of the other genera fit more deeply against similar, but generally faint, ridges. The axial ridge of *Gabrielona* very rarely is as deep in the aperture as shown in Pl. 52, fig. 3, ar. *Gabrielona* radulae are highly distinctive.

Taxonomic history—When Iredale proposed *Gabrielona*, he did “not think it has really any close relationship with *Phasianella*,” even though suggesting that it “may be classed for the present in the family Phasianellidae,” and “judging from the shell characters and the operculum and dead animal of the [unnamed] Lord Howe species . . . a Naticoid affinity suggests itself.” Characteristically, Iredale did not describe the genus or mention any distinguishing characters other than the naticoid operculum.

Retaining *Gabrielona* in the subfamily Phasianellinae, Thiele (1929) stated it to be doubtfully distinct from *Chromotis* H. and A. Adams, 1863. Following their description of what later came to be the type-species of *Gabrielona*, Gatliff and Gabriel (1908) had mentioned a similarity to *Phasianella neritina* Dunker—the type-species of *Chromotis*. Wenz (1938) retained *Gabrielona* as a tentative synonym of *Chromotis*, which he ranked as a subgenus of *Tricolia*. Australian malacologists have disregarded Thiele and Wenz, and have followed Iredale in treating *Gabrielona* as a distinct genus, but without giving reasons.

Finding that *Gabrielona* definitely is not a synonym of *Chromotis* (here considered a synonym of *Tricolia*), I re-established it, accorded it generic rank, and described it for the first time (Robertson, 1958). My study of the radula of “*G. brevis* (Orbigny)” [= *G. sulcifera* Robertson]—not the type species—revealed that it is rhipidoglossate but different from that in other Phasi-

anellidae. Thus, *Gabrielona* does not belong in the Naticidae or any other group with taenio-glossate radulae. Absence of a nacreous internal shell layer, and possession of a calcareous operculum necessitated my retaining *Gabrielona* in Phasianellidae, where I arbitrarily placed it in the subfamily Tricolinae.

Relationships—The relationships of *Gabrielona* to other supraspecific taxa in the Phasianellidae are obscure. The resemblances with most other phasianellids—shells of small size with bright colors and complex and variable patterns—seem superficial. In view of the distinct apertural, opercular and radular characters, the genus may not even belong in the family. However, pending more thorough knowledge of relationships within the Trochacea, it seems best to continue to retain *Gabrielona* in the Phasianellidae.

Shell description (abbreviations refer to the drawings)—Attains lengths of 1.1-3.3 mm., widths of 1.1-3.1 mm., and 3.0-4.6 whorls; spire angles 90°-125°; outlines globose; fairly thin to thick, and transparent to opaque. Protoconchs (p) insert to slightly exsert, slightly inflated, smooth or with a spiral keel, white, either not demarcated from teleoconch or slightly to fairly prominently demarcated, 0.9-1.2 whorls when demarcated. First whorls 0.20-0.29 mm. in diameter. Subsequent whorls: inflated, rounded in profile; suture slightly impressed. Sculpture predominantly smooth, or with axial plicae or spiral keels, cords and sulci; if present, sculpture most pronounced on second whorl, gradually declining and lacking near periphery or wholly lacking on last whorl of large shells. Periostracum not observed, but very thin layer possibly present. Colors: pinks, reds, or browns, and white. Patterns various, but commonly with subsutural, subperipheral, and peri-umbilical discordances. Aperture roundly pyriform; outer lip never thickened or everted, thin to thick; callus on upper parietal area thin to thick; a faint to fairly prominent axial ridge (ar) or series of faint ridges within the aperture (against which the fully withdrawn operculum abuts); the ridges fairly variable in position, but never distant from the edge of the outer lip; a fairly faint to fairly pronounced spiral palatal sulcus (ps) high in aperture or near middle, commonly positioned beneath a color pattern feature on external surface and terminating at apertural ridge. Depending on the species, 0-3 faint to rather prominent apertural denticles present, namely 1 palatal and opposite the shoulder in position (pd), 1 on the lower part of the columella (cd₂)—both these on the apertural ridge—

and 1 on the middle part of the columellar lip (**cd**₁); in species with a lower columellar denticle (**cd**₂), a faint, broad ridge spirals up the columella; apertural ridge, palatal sulcus, and apertural denticles fairly faint to lacking on small shells. Channel extending into umbilicus (**uc**) bordered on right by the outer edge of the columellar lip (a slope or an escarpment), and on the left (at an acute angle) by a fairly faint to prominent escarpment arising from the outer edge of the lower half of the columellar lip (abnormally, escarpment absent); umbilicus narrow to wide.

Opercula—Unlike those of the two other genera in the Phasianellidae, the opercula of *Gabrielona* are externally concave. In view of the extreme rarity of live-collected *Gabrielona* in collections, it is convenient that these distinctive opercula are retained—albeit infrequently—in the apertures of some empty shells. The fresh opercula are fairly transparent and white. They all are paucispiral and have fine, irregular spiral and radial growth lines and wrinkles on the external and internal surfaces; this fine sculpture is not shown in the accompanying drawings except where specially prominent.

The external surface has a prominent spiral ridge near the edge (except the non-spiral columellar sector) and a flattish but slightly concave central region which can have a differently textured or sculptured outer, spiral area. On all *Gabrielona* opercula, a callus of varied thickness overlays the upper two-thirds or three-quarters of the central region. This callus covers all or most of the spiral suture, is thickest near the middle columellar edge of the operculum, and its lower margin (marked **c** on the drawings) is irregular and variable in position and height, with or without a distinct escarpment. Small opercula and the single one known of *G. sulcifera* have a thin or very thin callus and therefore the suture is clearly visible externally—as well as in transparency. In the different species, the spiral ridge and central region are variously sculptured. The non-spiral columellar edge of the operculum is beveled.

The internal surface of the operculum is relatively flat, but the central part of the last whorl near the columellar margin can be slightly concave. The early whorls are slightly raised, and a low, spiral escarpment is at the suture. The central area (at the axis) on all the species with opercula available (*G. nepeanensis*, *G. pisinna*, *G. raunana* [both subspecies] and *G. sulcifera*) is circular, crested at the perimeter, and 0.11–0.14 mm. in diameter—i.e., correlates neither with the

various diameters of the first whorl of the shell, nor with the maximum shell size attained by the various species. This circular central area can be conspicuously smoother, shinier, and more transparent than the remainder of the internal surface, and always bears a low, central boss. The operculum of *G. raunana* (both subspecies) differs from those of the other species in having structural radial lamellae near the edge. Muscle attachment scars are never clearly defined.

When fully withdrawn into the aperture, the operculum abuts against the apertural ridge (**ar**), and fits closely against the columellar lip as well as the inner surface of the outer lip. In those species possessing the two columellar denticles, the operculum pivots against the columellar lip between these. The slight differences between species in the form of the columellar lip account for the slight differences in the outline of the columellar margin of the opercula.

Anatomy—The very few live-collected specimens available all were preserved dry, so that the bodies were dried out and appressed against the outer shell wall in the aperture. In *G. pisinna*, the gut—distended with whitish, calcareous fragments—was conspicuous, fairly short and U-shaped, arising at the left, extending posteriad and bending to the right at a position about half of a whorl back from the outer lip, and then extending forward to the anus on the right near the outer lip. There was no indication of an enlarged stomach. The mantle edge appeared to be rather thick, but the total volume of the dried body seemed remarkably small. Jaws were not detected but could be present.

Radulae (*Pls. 42 and 57*)—I have been able to study the radulae of only *G. pisinna* and *G. sulcifera*. These differ greatly from other known phasianellid radulae and also from each other. The specimens from which the radulae of the two species were extracted were collected about 9,200 miles apart (New Caledonia and Antigua), and the size difference between their shells is considerable: the shell volume of *G. pisinna* is about 19-fold smaller than that of *G. sulcifera*. Relative to shell size, the radula of *G. pisinna* is rather longer and considerably wider than that of *G. sulcifera*. These differences in actual and relative sizes perhaps account for some of the great differences. In particular, the small absolute size (but not the greater relative width) of the radula in *G. pisinna* could account for the fewer marginals and laterals (3 laterals instead of the 5 in *G. sulcifera*), and the more curved transverse rows of teeth. The “central” of *G. pisinna* possibly is a

pseudocentral comprised of one or two pairs of the original innermost laterals fused together (perhaps also with the original central).

The size differences could not account directly for some of the other interspecific differences: the multicusped laterals of *G. pisinna* and, in *G. sulcifera*, the unwinged central and laterals, the differently-shaped bases of the laterals, and the massive innermost marginals.

The radular differences help to confirm the conclusion reached independently from study of the shells and opercula of the two species, namely that they are distantly related congeners. Lacking information as to the total diversity of *Gabrielona* radulae, their possible ontogenetic changes, the structural consequences of their absolute and relative sizes, and bearing in mind the evolutionary plasticity of *Tricolia* radulae, I consider the radular differences inadequate evidence for separating *G. sulcifera* from *G. pisinna* in a different subgenus or genus.

Relationships within genus—Related pairs of Recent taxa are all allopatric. Only in New Caledonia is more than one species of *Gabrielona* known to occur, and these (*G. pisinna* and *G. raunana*) are distantly related congeners.

The most closely related taxa distinguished here are *G. raunana raunana* and *G. raunana goubini*, which are ranked as subspecies. *G. pisinna* is a dwarf, tropical Indo-Pacific homologue of southeastern Australian *G. nepeanensis*. *G. sulcifera* of the Caribbean perhaps is related, albeit fairly distantly, to the western Pacific *G. raunana*. *G. hadra* is a clearcut fossil precursor of *G. sulcifera*. *G. nepeanensis* and *G. pisinna* seem distantly related to their congeners.

Color and pattern variations—All the species are variable in coloration and pattern: *G. raunana* and *G. nepeanensis* especially so, and *G. pisinna* least of all. The range of coloration of *Gabrielona* is narrower than in each of the other two phasianellid genera. Most of the color and pattern variation in *Gabrielona* is gradational, but a discontinuous color variation is treated under *G. raunana goubini*.

Sexual dimorphism—Not detected conchologically.

Fossil history—The only fossil species known certainly to belong in the genus is "*Tricolia*" *hadra* Woodring from the Bowden Formation (Middle Miocene or possibly Pliocene-Pleistocene) in Jamaica, West Indies.

Distribution of Recent species—Until I transferred a West Indian species to the genus (Robertson, 1958), *G. nepeanensis* (Gatliff and Gabriel),

from southeastern Australia, was the only named species in the genus. An unnamed and cursorily studied *Gabrielona*, mentioned by Iredale (1917), was live-collected in the "sub-littoral" at Lord Howe Island (about 400 miles east of the coast of northern New South Wales, Australia). This locality, shown with a circle on Pl. 39, is between the known distributions of *G. nepeanensis* and the two tropical Indo-Pacific species. Iredale's specimens from Lord Howe were not located at the Australian Museum by Dr. D. F. McMichael in 1962 (letter to Dr. R. T. Abbott dated July 10).

One new tropical Indo-Pacific species, *G. pisinna*, and one new subspecies, *G. raunana goubini*, are described and named here, and the West Indian species to which I misapplied the name *Phasianella brevis* Orbigny is named *G. sulcifera*.

Gabrielona quite possibly occurs in other tropical and subtropical faunal areas, such as West Africa and the Panamic Province. The four known Recent species occur almost exclusively along the coasts of continents and high islands; the only known exception is *G. raunana raunana* Ladd, a subspecies known only as subfossil shells from an atoll.

Abundance—Very few live-collected specimens of any of the species have been available for study: only 7 *G. pisinna* and 1 *G. sulcifera*. The other two Recent species, including the type-species *G. nepeanensis*, are known only from empty, beach worn or subfossil shells, a few with opercula. Thus, the genus appears to be a relict group. Alternatively, it may have been rarely collected if, as I suspect, it mainly lives well below the tidal zone in algae on rocks.

Habitats—Known only from among algae in shallow water (*G. pisinna*) or in sand (*G. sulcifera*); for details see under these species. *G. pisinna* may live as deeply as 8 fathoms; a probably adventitious shell of *G. sulcifera* came from 287 fathoms.

Larval ecology—The fairly small range of variation in the diameter of the first whorls of the six known taxa of *Gabrielona* (0.20-0.29 mm.) and the small sizes presumably indicate that the full-grown larval shells are small and relatively uniform in size, and that the larvae are all pelagic and planktotrophic.

Abnormalities—A striking series of abnormalities possibly caused by an individual living in an unusual habitat is described under *G. sulcifera*. Abnormal growth caused by incrustations are rare in *Gabrielona*; one case is reported under *G. nepeanensis*.

Synonymy-

1917 *Gabrielona* Iredale, Proc. Malac. Soc. London 12:322 [listed], 327. Type-species (by monotypy): *Phasianella nepeanensis* Gatliff and Gabriel, 1908.—1929, Thiele, Handb. syst. Weichtierkunde, Jena, 1:70.—1938, Wenz, Handb. Paläozool., Berlin, 6(1):Teil 2 [Prosobranchia], p. 362.—1958, Robertson, Johnsonia 3(37):246-260.

Excluded species—In 1958 (pp. 253, 257), I suggested that three American Miocene (or Pliocene) species might belong in *Gabrielona*: *Tricolia* (*Eulithidium*) *hadra* Woodring, *Didianema* ? *waltonia* Gardner, and *Tricolia* ? *syn-toma* Woodring. *T. hadra* is here referred definitely to *Gabrielona*, but subsequent study of the holotypes of the other two species has shown that neither belongs in the Phasianellidae. Two upper Tertiary species from northern Venezuela described as *Gabrielona* are treated under *Excluded Species* on p. 61.

The possible second Western Atlantic Recent species of *Gabrielona* (Robertson, 1958, p. 259), from Brasil, proves upon restudy to be a depauperate, low-spined *Tricolia*.

Gabrielona nepeanensis (Gatliff and Gabriel, 1908)

(Pls. 36-39)

Range—Recent: known only from South Australia and Victoria, Australia. Possibly occurs also at Tasmania, but not yet known there.

Chief distinguishing characters—The shell differs from those of all other known species in the genus except *G. pisinna* in having both columellar denticles (cd_1 and cd_2), in lacking axial or spiral sculpture, and in opercular characters (see under *G. raunana* and *G. sulcifera* for differences). Differs from all other species, including *G. pisinna*, by its complex and varying but consistently distinct color patterns (the adults always with a colorless spiral band opposite the palatal sulcus). For detailed differences from *G. pisinna*, the most similar species, see under that species.

Abundance—36 shells from beach sand available, 1 with operculum in place in aperture; none live-collected (probably lives below the tidal zone).

Abnormal shell—One shell (Pl. 36, fig. 6) has a double outer lip near the suture, a columellar callus slightly detached from the palatal area, and the upper columellar denticle (cd_1) fainter than usual. Some incrustation must have interfered with normal growth.

Shell description—Attains length of 1.9 mm., width of 1.7 mm., and 3.9 whorls; spire angle 95° - 105° ; length invariably equals or exceeds width (except for small shells); fairly thick but slightly translucent to fairly transparent. Protoconch insert, slightly inflated, smooth, white, not demarcated from teleoconch. First whorl 0.24-0.28 mm. in diameter. Penultimate and last whorls: slight flattening below suture but no distinct shoulder (Pl. 38, fig. 1); surface smooth except for axial growth lines and slight wrinkles, fairly shiny. Colors: pale to dark pink (rarely, tinged with orange), and white. Patterns: alternating pink and white subsutural marks, each becoming divided by a virtually colorless spiral band directly opposite the palatal sulcus; 9-12 paired pink marks on last whorl; predominant below subsutural area: axially aligned wavy pink stripes or irregular marks; subperipheral series fairly faint pink and white marks; inner umbilical area colorless, surrounded by spiral series short white axial stripes (commonly, partially coalesced); rarely, zigzag pale pink stripes or irregular marks entirely replace usual pattern (Pl. 36, figs. 3-4). Outer lip and callus on upper parietal area fairly thin; no palatal denticle; palatal sulcus high in aperture; both columellar denticles present, most prominent on large shells (Pl. 38, fig. 2). Columellar lip thickened adjacent to central part umbilical channel, and an escarpment present; escarpment to left of umbilical channel fairly flat to prominent, arising fairly low off the outer edge of columellar lip; umbilicus narrow to fairly wide.

Shell measurements (mm.).—

length	width	no. whorls	
1.92	1.66	3.9	large: South Australia
1.56	1.46	3.3	average: South Australia
0.80	0.87	2.5	smallest: South Australia



Plate 37. *Gabrielona nepeanensis* (Gatliff and Gabriel). Victoria, Australia. Original figures of holotype (from Gatliff and Gabriel, 1908, pl. 21, figs. 9-10), enlarged. Both x20. Fig. 1 incorrectly shows a prominent shoulder (compare Pl. 36, fig. 10).

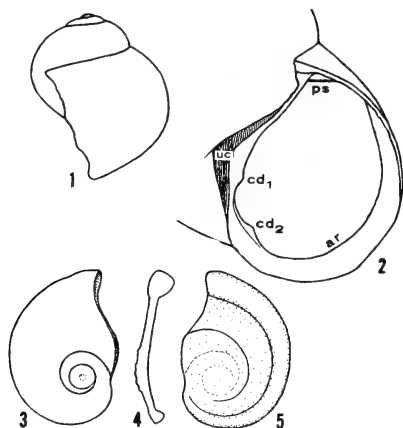


Plate 38. *Gabrielona nepeanensis* (Gatliff and Gabriel). Fig. 1. Outline of large shell, x17. Fig. 2. Aperture, x33; ar, apertural ridge; cd_1 and cd_2 , upper (outer) and lower (inner) columellar denticles (respectively); ps, palatal sulcus; uc, umbilical channel. Figs. 3-5. Operculum. Internal surface, longitudinal section, and external surface (respectively). All x33.

Operculum—(Pl. 38, figs. 3-5). Only a single, abraded operculum of this species has been available, and it has been difficult to determine the sculpture of its external surface. The crest of the spiral ridge near the edge seems to be rounded, and on the central region—between the outer, spiral area and the central area—there is a low, spiral ridge extending to a prominence on the non-spiral columellar margin. The outline of the columellar margin at the junction of the spiral and non-spiral sectors is shallowly concave. Otherwise the operculum of *G. nepeanensis* seems to be like that of *G. pisinna*, only larger; both are fairly thin.

Synonymy—

- 1908 *Phasianella nepeanensis* Gatliff and Gabriel, Proc. Roy. Soc. Victoria, n.s., 21(1): 366, pl. 21, figs. 9-10 [reproduced here, Pl. 37] (Flinders, Western Port; Ocean Beach, near Point Nepean [both Victoria, Australia]).
—1917, Iredale, Proc. Malac. Soc. London 12(6): 322 [listed], 327 [the only named species included in *Gabrielona* but not formally transferred].
1938 *Gabrielona nepeanensis* (Gatliff and Gabriel), Cotton and Godfrey, Malac. Soc. South Australia Publ. 1: 9; 1945, Cotton, Trans. Roy. Soc. South Australia 69(1): 165; 1958, Robertson, Johnsonia 3(37): 257, pl. 137, figs. 2-3, pl. 140, fig. 1; 1959, Cotton, South Australian Mollusca, Archaeogastropoda, Adelaide, pp. 270-271, fig. 185 [shell shape highly inaccurate], p. 347 [listed].

Types—The holotype of *Phasianella nepeanensis* Gatliff and Gabriel (Pl. 36, fig. 10; Pl. 37) is now at the National Museum of Victoria (no. F543), Melbourne, Australia. A small paratype is at the Australian Museum (no. C.45057), Sydney (Robertson, 1958, pl. 140, fig. 1). Gatliff and Gabriel did not mention the number of specimens available to them, and recorded the species from two localities 23 miles apart. Cotton and Godfrey (1938) selected "Flinders, Victoria" as the type-locality. However, in 1945 and subsequently, Cotton has stated that the type-locality is "near Point Nepean," whence (judging by the specific name) the holotype came.

Locality records (see map, Pl. 39; literature and uncertain records circled)—SOUTH AUSTRALIA: Port Lincoln ("apparently *nepeanensis*," Iredale, 1917; Cotton, 1945); Mouth of Middle River, N. coast Kangaroo I. (from beach sand, 1954, B. Daily, via M. F. Glaessner and G. L. Harrington); Port Adelaide (Calvert Coll., both ANSP); Robe (Cotton, 1945). VICTORIA: Port Fairy (in beach sand, 1923, H. A. Pilsbry, ANSP); ocean beach near Point Nepean [38 mi. S.S.W. of Melbourne] (Gatliff and Gabriel, 1908; Natl. Mus. Vict.; Austral. Mus.); Flinders [47 mi. S. of Melbourne], Western Port (Gatliff and Gabriel, 1908).

All three of the circled locality records in South Australia are questionable because Cotton (1945, 1959) mentioned having difficulty distinguishing *G. nepeanensis* from "*Pellax virgo*," and the locality data with all the available specimens except one juvenile shell from Kangaroo Island seem not wholly reliable either. A large series (30 shells) is from the Calvert Collection (collector not recorded), labeled "Pt. Adelaide" is suspect because this is the largest port in the area.

Gabrielona pisinna Robertson, new species

(Pls. 39-42)

Range—Recent: known only from Mauritius, Indian Ocean, and New Caledonia, eastern Melanesia. Perhaps widespread in the tropical Indo-Pacific around high islands.

Chief distinguishing characters—The shell, usually less than 1 mm. in length, is full-grown at a smaller size than in any other known phasianellid. It resembles young *G. nepeanensis* in size and number of whorls. (Further resemblances: has both columellar denticles, an unsculptured surface, and a similar operculum.) That *G. pisinna* is full-grown at a smaller size than *G. nepeanensis* is shown by the complete development on the larger shells of the lower columellar denticle (cd_2). Further differences from *G. nepeanensis*: first whorl smaller; spire lower (except for some

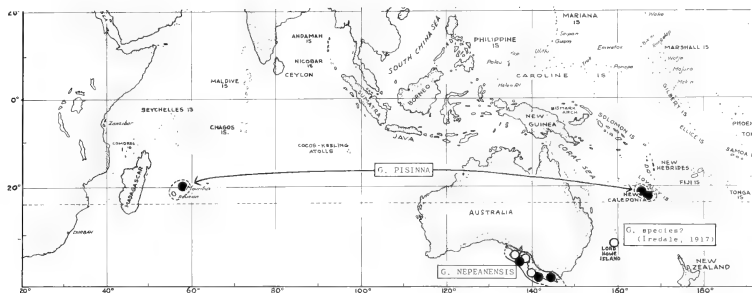


Plate 39. Geographical distributions and records of *Gabrielona nepeanensis* (Gatliff and Gabriel), *Gabrielona* species? (Iredale, 1917), and *Gabrielona pisinna* Robertson, which

large shells, the width of *G. pisinna* invariably exceeds the length; aperture smaller than in young *G. nepeanensis* of comparable size (compare Pl. 40 with Pl. 36, fig. 1); color patterns different (finer), and reddish coloration darker.

Relationships—A dwarf, tropical homologue of *G. nepeanensis*, which might need to be ranked as a subspecies if the form occurring at Lord Howe Island (map, Pl. 39) is intermediate (see p. 44).

Abundance—68 specimens available: 2 empty shells from Mauritius (1 with operculum), and 66 specimens from New Caledonia (10 with opercula, 7 of these live-collected).

Habitat—All 7 of the live-collected specimens came from washings from algae collected in 0-3 ft. on Récif Ricaudy, New Caledonia, on rocks near shore on the fringing reef. An empty but fresh shell with 4 drill holes and an operculum in place in the aperture came from a depth of 8 fathoms at Mauritius (see under *Locality records*). (Many of the shells have these drill holes.)

Shell description—Attains length of 1.1 mm., width of 1.1 mm., and 3.0 whorls; spire angle 115°-125°; width exceeds length (excepting some large shells); fairly thin and translucent to transparent. Protoconch insert, slightly inflated, smooth, white, not demarcated from teleoconch. First whorl 0.20-0.24 mm. in diameter. Penultimate and last whorls: slight flattening below suture but no distinct shoulder (Pl. 41, figs. 2-3); surface smooth except for axial growth lines and slight wrinkles, shiny; fine spiral sulci on base of small shells (Pl. 41; fig. 1). Colors: dark pink to bright red (rarely, tinged with amber [faded?]), and white. Patterns: white spiral band below the suture, coalescing with variably-shaped white subsutural patches (7-9 on last whorl), lower

perhaps is widespread in the tropical Indo-Pacific but which presently is known only from the two areas 7300 miles apart.

edges of which are slightly below or directly opposite the palatal sulcus; pink or red marks or non-axial stripes alternate with white subsutural patches; predominant below subsutural area: fairly regular axial or very steeply ascending dark stripes; subperipheral series of white marks alternating with non-axial dark stripes or axially paired marks; umbilical area closely surrounded by spiral series of short white axial stripes (fairly commonly, partially coalesced); very rarely, subsutural patches and subperipheral white marks coalesce into irregular axial white bands (Pl. 40, fig. 2). The aperture averages relatively

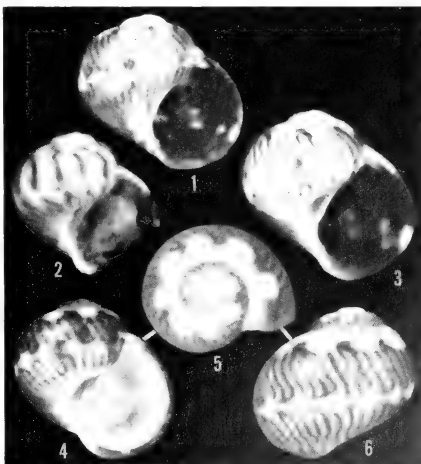


Plate 40. *Gabrielona pisinna* Robertson. Fig. 1. Mauritius. Figs. 2-6. New Caledonia. Figs. 4-6. Holotype. All x30.

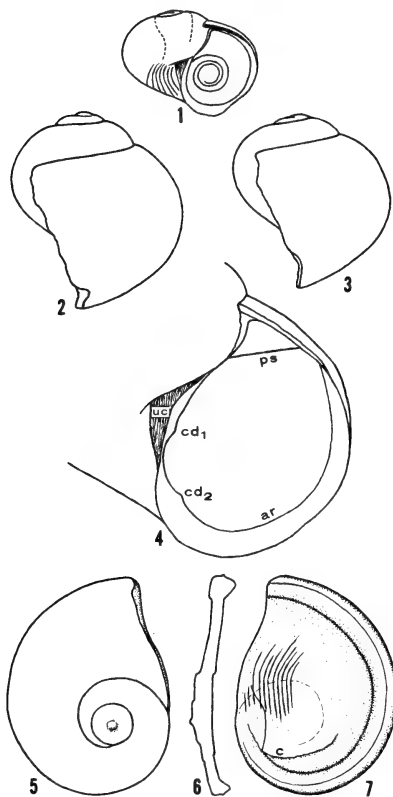


Plate 41. *Gabrielona pisinna* Robertson. Fig. 1. Smallest specimen, x60. Figs 2-3. Outlines of largest shells, both x33. Fig. 2. Unusually high-spired shell. Fig. 4. Aperture, x60; ar, apertural ridge; cd₁ and cd₂, upper (outer) and lower (inner) columellar denticles (respectively); ps, palatal sulcus; uc, umbilical channel. Figs. 5-7. Operculum. Internal surface, longitudinal section, and external surface (respectively); c, lower edge of callus. All x60.

slightly wider than in *G. nepeanensis*. Outer lip and callus on upper parietal area thin; no palatal denticle; palatal sulcus high in aperture, slightly variable in position (commonly, fairly faint); both columellar denticles present, most prominent on large shells (Pl. 41, fig. 4). Columellar lip slightly thickened adjacent to central part umbilical channel, and an escarpment, when present, faint; escarpment to left of umbilical channel fairly prominent, arising fairly low off outer edge columellar lip; umbilicus fairly wide.

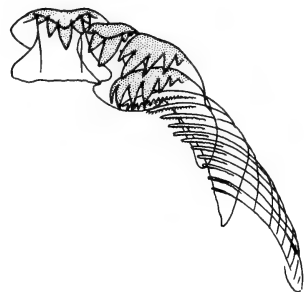


Plate 42. *Gabrielona pisinna* Robertson. Half of one transverse row of radular teeth, showing (from left to right) the 5-cusped central (or pseudocentral?), the three laterals on the right side, and the entire row of marginals. The cusps of the central and laterals are stippled. New Caledonia. x1050.

Shell measurements (mm.)—

length	width	no. whorls	
1.09	1.10	3.0	largest; New Caledonia
0.91	0.93	2.8	holotype; New Caledonia
0.70	0.75	2.6	average; Mauritius
0.34	0.42	1.7	smallest (Pl. 41, fig. 1); New Caledonia

Operculum—(Pl. 41, figs. 5-7). The spiral ridge near the edge on the external surface of the fairly thin operculum is sharply crested except near the columellar margin where it is rounded. The inner margin of the ridge is angled or rounded. The central region has an outer, spiral area with a mat surface contrasting with a shiny, more transparent central area. The single operculum available from Mauritius differs from those from New Caledonia in having a faint spiral ridge between the two areas (like that of *G. nepeanensis*). Fairly prominent wrinkles parallel to the non-spiral columellar margin are present to the left of the central part of the callus. The lower margin of the callus (c) varies in position.

Radula (Pl. 42; 2 studied)—Attains length of 0.37 mm., width of 0.08 mm., and with as many as 20 very strongly curved transverse rows of teeth (including a few nascent rows). Central (or pseudocentral?) 5-cusped, laterally winged anteriorly, and with posterolateral projections on the base. Three laterals, each with long pointed cusps (the two innermost generally with 5 cusps, and the outermost with 6); the two outermost laterals have the largest distal portions, and the outer lateral is positioned posterior (rather than lateral) to the morphologically middle lateral; the

base of the innermost lateral bears a posterolateral peg that fits into the middle of the inner edge of the base of the middle lateral, and the two outermost laterals have large bases that extend posterolaterally beneath the marginals. As many as 13 pairs of marginals (lowest count 10), each row widely overlapping the row posteriorly. All the marginals have elongate distal portions, and the innermost of these are serrate on the outer (posterior) edge; the serrations become finer outwards and are absent altogether on the small outermost teeth.

Types—The holotype (Pl. 40, figs. 4-6), from Récif Ricaudy, near Noumea, New Caledonia, is at the Academy of Natural Sciences of Philadelphia (no. 301611). So also are paratypes from the type-locality (no. 271062) and from other localities: Récif de Gatope, New Caledonia (nos. 267567 and 267568), and Mauritius (nos. 273188 and 273328). Paratypes from New Caledonia will be distributed to USNM, MCZ, BM, and IrSnB (2 shells each).

Derivation of new name—Latin, *pisinnus*, little.

Locality records (see map, Pl. 39)—MAURITIUS: $\frac{7}{8}$ mi. N.N.E. of Flic en Flacq Pt. (1-10 ft., from *Caulerpa* washings, Nov., R.E.M. Ostheimer & V. Orr Maes, Sta. M 203); Black River Bay, 1 mi. W.N.W. of mouth Black River, both W. coast (dredged 8 fms. [1 empty but fresh shell], coarse sand, broken shell, very little weed, Nov. 5, both 1960, R.E.M. Ostheimer, J. de B. Baissac & V. Orr Maes, Sta. M 208, both ANSP). NEW CALEDONIA: Grand Récif de Gatope, $\frac{7}{8}$ mi. W. of Voh (dredged 6-18 ft., inner edge of barrier reef, sand, weed, coral rubble, Dec. 31, 1960 & Jan. 2, 1961, Stas. K 538 & K 539); E. end Récif Ricaudy, $\frac{2}{3}$ mi. S.S.E. of Noumea (0-3 ft., Jan. 11, 1961, both G. & M. Kline & V. Orr Maes, Sta. K 553, both ANSP).

Gabrielona raunana Ladd, 1966

(Pls. 43-50)

Range—Recent: known only from Eniwetok (an atoll), northwestern Marshall Islands (*G. raunana* Ladd), and from the Loyalty Islands and New Caledonia (all high islands), eastern Melanesia (*G. raunana goubini* Robertson).

Chief distinguishing characters—This is the only species in the Phasianellidae having a shell with prominent axial sculpture. The plicae are most prominent and regularly arranged on the second whorl, and are obscure or absent at and near the periphery of the last whorl of large shells. Also differs from other species in the genus as follows: spiral keel on protoconch; all apertural denticles lacking; operculum with obliquely radial sulci on part of external surface, and with

structural radial lamellae at and near the spiral outer edge. The outlines of the shells and color patterns of both subspecies are distinct from each other and from those of the other species.

Remarks—No live-collected specimens are available of either subspecies; most of the shells are beach worn or subfossil. *G. raunana*, known only from populations in two areas slightly more than 2,000 miles apart, seems thus to be a relict species.

Shell descriptions, Types, Locality records, etc.—See under *G. raunana raunana* and *G. raunana goubini*.

Operculum (Pl. 44)—Only 2 opercula of *G. raunana raunana* and 8 of *G. raunana goubini* are available, and because all these are abraded or corroded—making description and illustration of the original sculpture difficult—and because it is doubtful whether the seeming slight differences between the two subspecies are real, they are discussed together here. The operculum in best condition is a small one from *G. raunana raunana*.

Relative to those of *G. nepeanensis* and *G. pisinna*, the operculum of *G. raunana* (both subspecies) is thick and comprises fractionally more whorls (comparing opercula of the same size). The external surface has a central region with an outer, spiral area distinctive in having prominent, obliquely radial sulci (irregular and varying in spacing), and a central, smoothish area with a fairly thick callus. The crest of the spiral ridge is

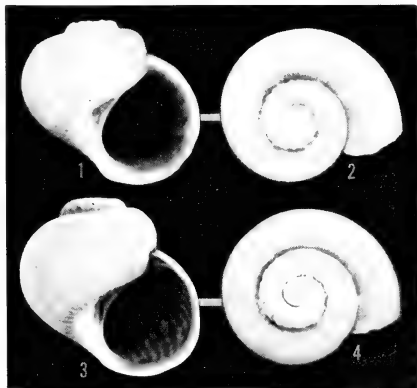


Plate 43. *Gabrielona raunana* Ladd. Thinly coated with magnesium oxide to accentuate the sculpture and obscure the color pattern. Figs. 1-2. *G. raunana raunana* Ladd. Eniwetok, Marshall Islands. Figs. 3-4. *G. raunana goubini* Robertson. Lifou, Loyalty Islands. All x20.

near the outer edge, and (at least on *G. raunana raunana*) its whole surface is irregularly wrinkled and knobbed, the wrinkles tending to be aligned with the adjacent obliquely radial sulci.

The erosion of the external surface makes several features obscure. The spiral ridge is strongly abraded on all the opercula available from *G. raunana goubini*. On all but one of these there is a deep but irregular central pit that may be an erosional feature; this is margined by an irregular but steep escarpment at the lower margin of the callus (c). On the unpitted operculum of *G. raunana goubini*, two spiral sulci are near the center and there is no steep escarpment bordering the callus; this perhaps is the uneroded original sculpture.

Seen in transparency, near the outer edge of the operculum are structural radial lamellae at right angles to the horizontal plane of the operculum. These are closely and regularly spaced and extend a uniform distance from the edge. Most prominent at the edge of the operculum of *G. raunana raunana*, these project from the surface as external lamellae, thus causing the outline to be finely notched. These external lamellae perhaps are erosional features.

***Gabrielona raunana raunana* Ladd, 1966**

(Pl. 43, figs. 1-2; Pl. 44, figs. 4-6; Pls. 45-47)

Range—Recent: known only from subsurface deposits on Eniwetok Atoll, northwestern Marshall Islands (obtained from drillings). Perhaps widespread at atolls in Micronesia or the whole tropical northwest Pacific.

Chief distinguishing characters—The shell of this subspecies has fairly regularly spaced but

commonly coalesced colorless or white spots, each one surrounded by 6 others. More differences are given under *G. raunana goubini*. Sculpture is almost identical in the two subspecies.

Abundance—32 subfossil shells available, 1 with an operculum in place in the aperture; 1 loose operculum.

Shell description—Attains length of 2.1 mm., width of 2.1 mm., and 3.4 whorls; spire angle 110°-125°; width invariably equals or exceeds length; fairly thick to fairly thin and opaque to fairly transparent. Protoconch insert, smooth except for slightly descending spiral keel, white, slightly demarcated from teleoconch, 0.9 whorl. First whorl 0.26-0.29 mm. in diameter. Penultimate and last whorls: flattening below suture, and faint shoulder (Pl. 46, fig. 1). Sculpture of second whorl: 18-30 strong axial plicae, convex towards outer lip, highest, most sharply crested and most widely spaced on first half where a fairly prominent to fairly obscure spiral cord extends from the keel on protoconch. On later whorls plicae smaller, crests rounded, more closely spaced, and less regular in arrangement and structure, commonly with intercalated secondary plicae below suture and with divarications and anastomoses below periphery. A faint spiral cord surrounds the umbilical area of young shells; rarely, faint reticulations on base of medium-sized shells. On last whorl irregular axial plicae most prominent below suture and on base, absent near periphery of large shells where surface is smooth except for axial growth lines. Surface shiny. Colors: pale (faded?) to fairly pale pink or yellowish brown, and white. Patterns: more or less quadrate pink or brownish subsutural patches (6-10 on last whorl), lower edges directly opposite palatal sulcus; surface almost entirely covered with fairly regularly spaced spots, each one sur-

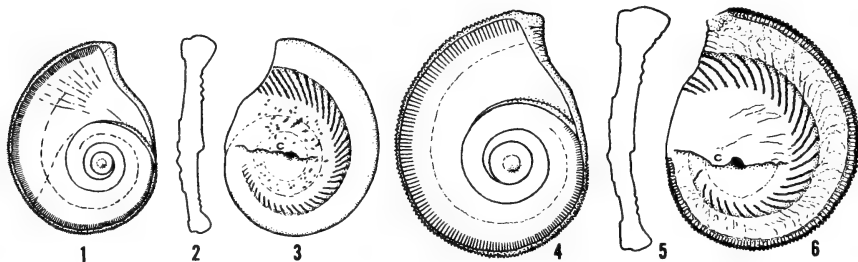


Plate 44. *Gabrielona raunana* Ladd. Opercula. Figs. 1-3. *G. raunana goubini* Robertson, x33. Figs. 4-6. *G. raunana raunana*, x60.

Internal surface, longitudinal section, and external surface of each; c, lower edge of callus.

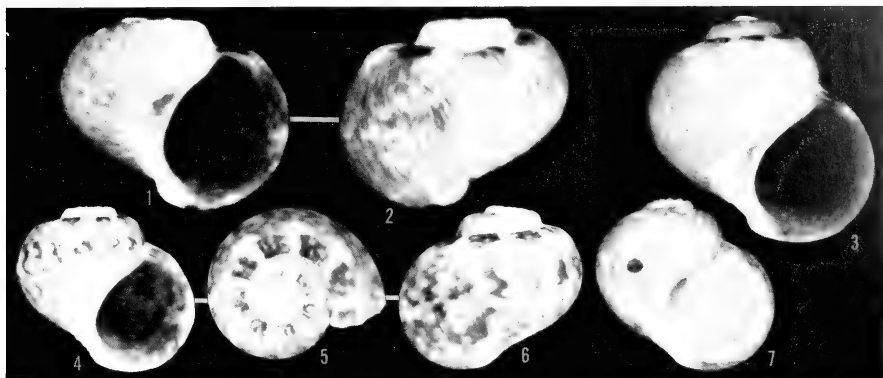


Plate 45. *Gabrielona raunana raunana* Ladd. Subsurface Recent deposits, Eniwetok Atoll, Marshall Islands. Fig. 7. Holotype. Figs. 1-2, x40; Figs. 3-7, x20.

rounded by 6 others; spots white in pale areas alternating with subsutural patches and colorless elsewhere except (somewhat commonly) for sub-peripheral spiral series and (rarely) spiral series on base; commonly: spots irregularly coalesced; ground color pale; fairly commonly: subperipheral spiral series irregular, slightly darkened markings alternating with white-spotted areas; closely surrounding umbilicus: spots variously coalesced into irregular, steeply descending white stripes on colorless ground; fairly rarely: wavy, axial darkened bands extending from subsutural patches to base; rarely: almost a uniform pink with no spots near periphery. Outer lip and callus on upper parietal area somewhat thin to fairly thick; no palatal denticle; palatal sulcus high in aperture,

neither columellar denticle present (Pl. 46, fig. 2). Columellar lip not thickened, and steep slope into umbilical channel but no escarpment; escarpment to left of umbilical channel prominent, arising quite high off the outer edge of the columellar lip; umbilicus fairly narrow to wide (Pl. 46, fig. 2).

Shell measurements (mm.).—

length	width	no. whorls	
2.09	2.09	3.4	largest
1.60	1.67	3.1	average; holotype
0.89	1.07	2.4	smallest

Operculum—See under *G. raunana* (species).

Synonymy—

1966 *Gabrielona raunana* Ladd, [U.S.] Geol. Surv. Prof. Paper 531, pp. 13 & 17 [listed], 54 [described], pl. 10, figs. 1-5 (Recent, Eniwetok Atoll).

Types—The holotype (Pl. 45, fig. 7), out of a drilling from 20-45 ft. below land surface Elugelab, Eniwetok, is at the United States National Museum (no. 648319), Washington, D.C. So also are all the paratypes except 3 donated to the Academy of Natural Sciences of Philadelphia (no. 302131).

Locality records (see map, Pl. 47)—MARSHALL ISLANDS: Elugelab (20-60 ft. deep), Parry (30-45 ft., 90-110 ft., 1865-1895 ft.), and Mujinkarikku (35%-40% ft.), all Eniwetok Atoll (from 8 drill holes in Recent subsurface deposits; 30 shells and 1 loose operculum at depths of 20-60 ft., 1 shell from 90-110 ft., and 1 probably adventitious shell in lower Miocene strata at 1865-1895 ft., all about 1952, U.S. Ladd, USNM & ANSP). For an account of the drilling operations which yielded most of the specimens, see Ladd and Schlanger (1960, [U.S.] Geol. Surv. Prof. Paper 260-Y, pp. i-iv, 863-905).

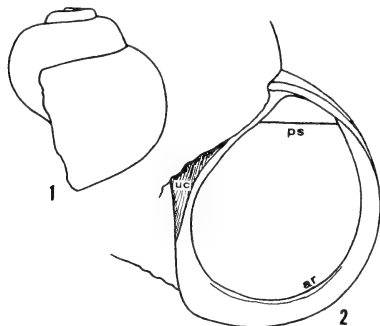


Plate 46. *Gabrielona raunana raunana* Ladd. Fig. 1. Outline of large shell, x17. Fig. 2. Aperture, x33; ar, apertural ridge, ps, palatal sulcus; uc, umbilical channel.

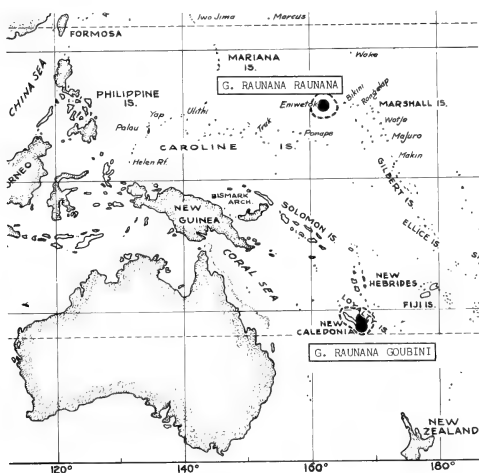


Plate 47. Geographical records of *Gabrielona raunana raunana* Ladd and *Gabrielona raunana goubini* Robertson.

***Gabrielona raunana goubini*
Robertson, new subspecies**

(Pl. 43, figs. 3-4; Pl. 44, figs. 1-3; Pls. 47-50)

Range—Recent: known only from Lifou, Loyalty Islands, and Ile des Pins, New Caledonia, eastern Melanesia. Perhaps widespread around high islands in Melanesia or the whole tropical south-west Pacific.

Chief distinguishing characters—The shell differs from that of the nominate subspecies as follows: spire averages higher and aperture relatively smaller; first whorl averages smaller; plicae finer on medium-sized shells; color pattern almost invariably with steeply descending pink or yellowish brown stripes, and white subsutural patches commonly ring-shaped.

Abundance—1,116 shells available, 8 with an operculum in place in the aperture. All the specimens were sorted from beach sand; some are freshly dead, but many are worn or broken and some are bleached.

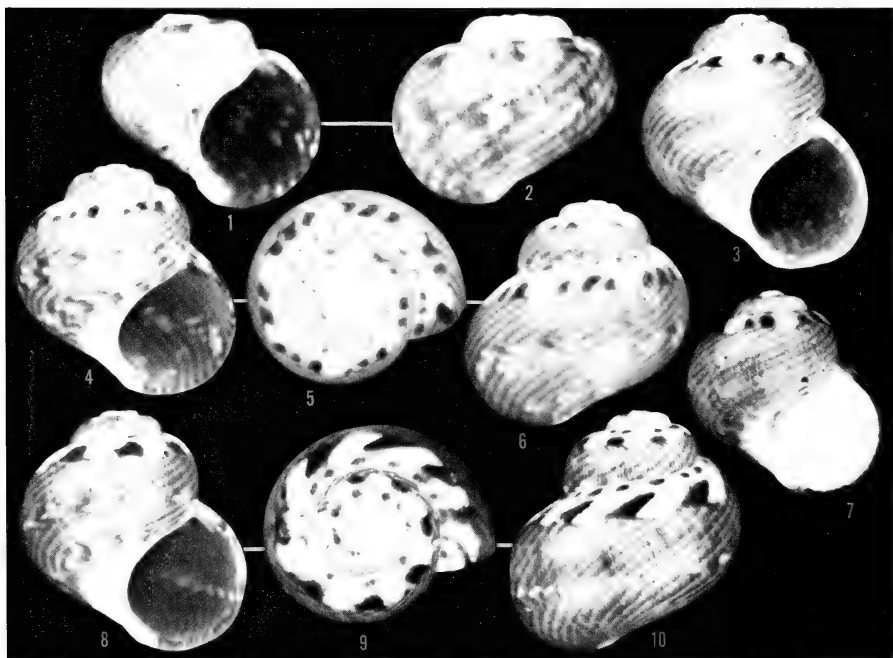


Plate 48. *Gabrielona raunana goubini* Robertson. Lifou, Loyalty Islands. Fig. 7. Holotype. Figs. 1-2, x40; Figs. 3-10, x20.

Remarks—In view of the apparent abundance of this subspecies in beach sand it is remarkable that it has not been named previously, in spite of rather extensive study of small marine shells from the Loyalty Islands (Tomlin, 1936, Proc. Malac. Soc. London 22(3): 145-152).

Color variation—Most of the shells have pink markings; an infrequent color form is entirely devoid of pink and has pale yellowish brown markings; intermediates have the pink followed by the yellowish markings. Only a few shells were not readily sorted into one of these three categories. Of the 1,088 shells from Lifou, approximately 938 (86%) are the pink form, 112 (10%) are intermediates, and 38 (4%) are the yellowish form. The frequencies of the three color forms are comparable in the much smaller sample (28 shells) from Ile des Pins: 18 (64%) pink, 7 (25%) intermediates, and 3 (11%) yellowish.

Shell description—Attains length of 2.4 mm., width of 2.2 mm., and 3.9 whorls; spire angle 90°-115°; width fairly commonly exceeds length; fairly thick but slightly translucent to fairly transparent. Protoconch like that of *G. raunana raunana*. First whorl 0.23-0.28 mm. in diameter. Subsequent whorls: flattening below suture, and faint to obscure shoulder (Pl. 50, fig. 1). Sculpture like that of *G. raunana raunana* except plicae (Pl. 50, fig. 2) finer, spiral cord on first quadrant(only) of second whorl faint or absent, and no reticulations on base of medium-sized shells. Surface shiny. Colors: fairly pale to dark pink,

pale yellowish brown, and white. Patterns: variably-shaped white subsutural patches (7-9 on last whorl), commonly ring-shaped with axial stripe extending to suture, lower edges near or directly opposite palatal sulcus; white subsutural patches alternating with variable yellowish brown or pinkish marks; predominant below subsutural area: steeply descending pink and/or yellowish brown stripes; commonly: subperipheral series small, irregular white marks alternating with slightly darkened pinkish or yellowish brown marks; fairly commonly: similar series small white marks on base, with darkened pinkish marks; closely surrounding umbilicus: steeply descending, partially coalesced white stripes; very rarely: all descending stripes zigzag or broken into irregular marks (Pl. 49). Aperture averages slightly narrower and relatively smaller than that of *G. raunana raunana*; outer lip somewhat thick; callus on upper parietal area thin to fairly thick; apertural denticles, palatal sulcus, columella and umbilical area as in *G. raunana raunana*, except escarpment to left of umbilical channel fairly faint to prominent and umbilicus narrow to quite wide.

Shell measurements (mm.)—

length	width	no. whorls	
2.42	2.16	3.9	largest
1.92	1.80	3.5	average; holotype
0.90	1.01	2.6	smallest

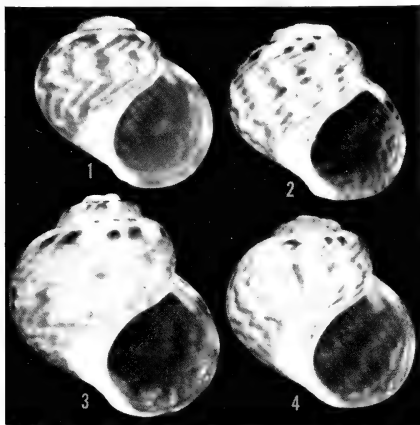


Plate 49. *Gabrielona raunana goubini* Robertson. Rare color patterns, Figs. 1-3. Lifou, Loyalty Islands. Fig. 4. Ile des Pins, New Caledonia. All x20.

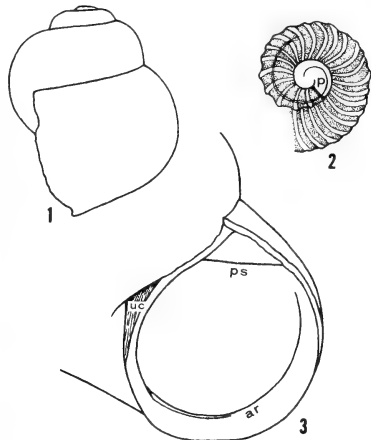


Plate 50. *Gabrielona raunana goubini* Robertson. Fig. 1. Outline of large shell, x17. Fig. 2. Apex, x33; p, protoconch. Fig. 3. Aperture, x33; ar, apertural ridge; ps, palatal sulcus; uc, umbilical channel.

Operculum—See under *G. raunana* (species).

Types—The holotype (Pl. 48, fig. 7) from Lifou, Loyalty Islands, is in the Dautzenberg Collection at the Institut royal des Sciences naturelles de Belgique, Brussels. So also are 1,102 paratypes from Lifou and Île des Pins. Ten more paratypes from Lifou are retained at the Academy of Natural Sciences of Philadelphia (no. 302624), and 3 from Lifou have long remained unidentified at the United States National Museum (no. 422601), Washington, D. C.

Derivation of new name—Named for Goubin, the collector who meticulously sorted out from beach sand 1,085 of the shells.

Locality records (see map, Pl. 47)—LOYALTY ISLANDS: Île Lifou (Goubin, IrSnB & ANSP; Moss, USNM). NEW CALLEDONIA: Île des Pins (Lambert, IrSnB).

***Gabrielona hadra* (Woodring, 1928)**

(Pls. 51-53)

Range—Middle Miocene or Plio-Pleistocene: known only from the Bowden Formation, southeastern Jamaica, Greater Antilles. Presumably was widespread in the Caribbean area. (On apparent endemism in the Bowden Formation, see W. P. Woodring, 1965, *Science* 148 (3672): 961-963.)

Chief distinguishing characters—The shell attained a larger size than that of any Recent species in the genus. *G. hadra* is distinct also in having a deeply embayed columellar lip below the junction with the palatal wall. Otherwise, *G. hadra* closely resembles *G. sulcifera* (the sculpture of the second whorl is similar, the palatal

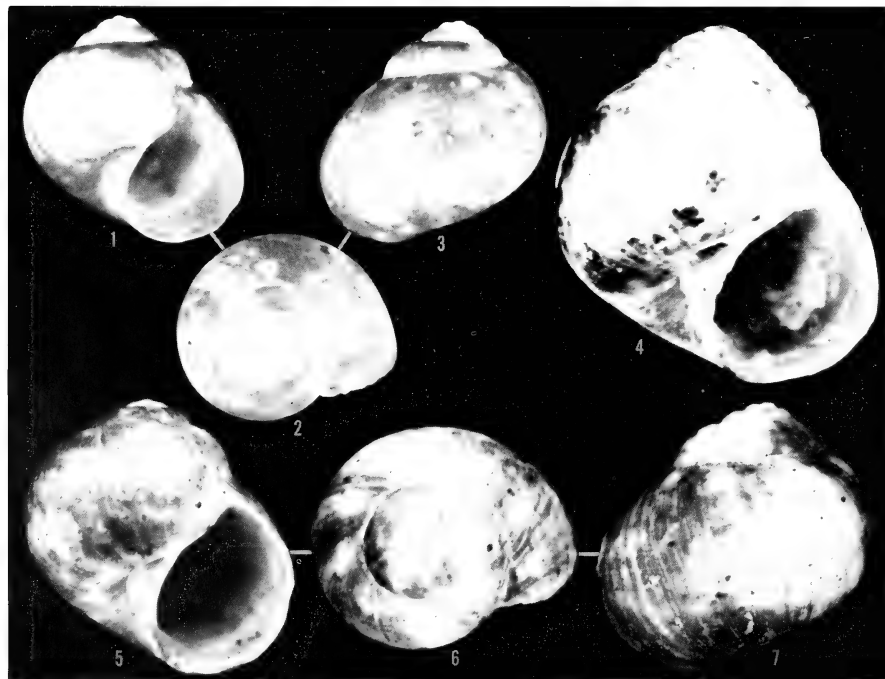


Plate 51. *Gabrielona hadra* (Woodring). Middle Miocene (or Plio-Pleistocene), Bowden Formation, Jamaica. Fig. 4. Large-

est known specimen of any *Gabrielona* (surface eroded). Figs. 5-7. Holotype. All $\times 20$.

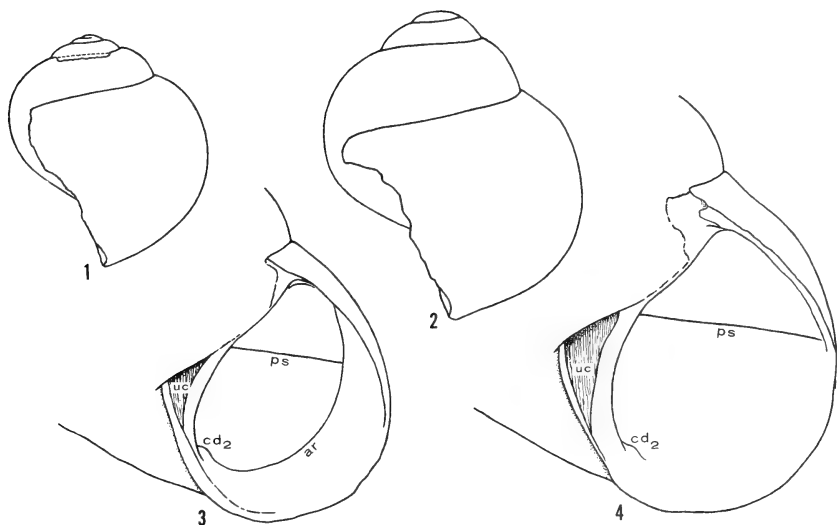


Plate 52. *Gabrielona hadra* (Woodring). Figs. 1-2. Outlines of shells, showing variation, both $\times 17$. Fig. 2. Largest known specimen of any *Gabrielona* (surface eroded). Figs. 3-4. Apertures, showing variation; both $\times 33$; ar, apertural ridge; cd₂, lower (inner) columellar denticle; ps, palatal sulcus; uc, umbilical channel. Figs. 1 and 4. Holotype.

sulcus is near the middle of the aperture, and only the lower columellar denticle (cd₂) is present). Additional differences from *G. sulcifera*: first whorl averages smaller; spiral sculpture on second whorl less prominent, disappearing before the beginning of the third whorl; no spiral sulci on later whorls; color patterns different.

Abundance—21 shells currently available, none with opercula (36 paratypes not available; see under *Types*).

Remarks—This is the only known fossil species undoubtedly belonging in the genus, and clearly is a precursor of the Recent Caribbean *G. sulcifera*. The relative abundance of *G. hadra* in the Bowden Formation is noteworthy in view of the rarity of its living descendant.

The surface of the shell is most resistant to corrosion where there were white markings, which on some shells are preserved as low projections.

Shell description—Attained length of 3.3 mm., width of 3.1 mm., and 4.6 whorls; spire angle 95°-120°; length invariably exceeds width (except possibly for small shells), but outline variable; fairly thick to thick, and opaque (fresh

shells might be translucent or transparent). Protoconch slightly exsert, slightly inflated, smooth, whitish, slightly demarcated from teleoconch, 1.1-1.2 whorls. First whorl 0.23-0.25 mm. in diameter. Penultimate and last whorls: slight flattening below suture and faint shoulder (Pl. 52, figs. 1-2). Sculpture of second whorl: 3 fairly low spiral keels on first quadrant following protoconch, each about equal in prominence; keels gradually becoming spiral cords, commonly with 2 more cords intercalated; very fine axial threads; all sculpture gradually disappearing on third or fourth quadrant, commonly with no spiral sulci; on later whorls surface wholly smooth except for fine axial growth lines. Surface shiny. Colors: pale (faded?) reddish or purplish brown, and white. Patterns: irregularly shaped whitish subsutural patches (8-11 on last whorl), alternating with brownish areas; lower edges of patches irregular, not correlated with position of palatal sulcus; predominant below poorly demarcated subsutural area; ground color pale reddish brown; 2-3 spiral series irregular white markings (commonly crescentic, concave towards outer lip) that are smaller than the subsutural patches; 2 of these series near (above and below) periphery (upper one fairly uncommonly absent), and third on base (6-9 markings); umbilical area commonly tinged with purple. Aperture shape like

that of *G. sulcifera*; outer lip fairly thin to thick; callus on upper parietal area thin to thick; palatal denticle absent; apertural ridge (ar) shallow to fairly deep in aperture (Pl. 52, fig. 3); palatal sulcus near middle of aperture; upper columellar denticle (cd₁) absent; lower columellar denticle (cd₂) present, prominent or low and wide (Pl. 52, figs. 3-4). Columellar lip not thickened, deeply embayed below junction with palatal wall; fairly shallow slope into wide umbilical channel; escarpment to left of umbilical channel prominent, arising fairly high to high off outer edge columellar lip, and commonly the right-hand edge of a ridge; umbilicus wide.

Shell measurements (mm.)—

length	width	no. whorls	
3.30	3.06	4.6	largest
2.51	2.44	4.2	average; holotype
2.10	2.04	4.0	fairly small

Synonymy—

1928 *Tricolia* (*Eulithidium*) *hadra* Woodring, Carnegie Inst. Washington Publ. 385 (Miocene Mollusks from Bowden, Jamaica; Part II), pp. 16 [name listed], 420-421, pl. 34, figs. 10-11.—1958, Robertson, *Johnsonia* 3(37): 253, 257 [provisionally referred to *Gabrielona*].

Types—The holotype of *Tricolia* (*Eulithidium*) *hadra* Woodring (Pl. 51, figs. 5-7), from near Bowden, Jamaica, is at the United States National Museum (no. 369556), Washington, D.C. This presumably was one of the "37 specimens in the Duerden Collection" mentioned by Woodring,

The remaining 36, which can be considered paratypes, were not found in the paleontological collection from Johns Hopkins University on deposit at USNM (May, 1965). Twenty topotypes from the Henderson collection are at USNM (no. 135509).

Fossil record (see map, Pl. 53, black triangle)—JAMAICA: near Bowden, St. Thomas Parish (1894, J.B. Henderson, Jr.; 1899, J.E. Duerden; in thin bed imperfectly consolidated gravel in a marly matrix; USNM).

***Gabrielona sulcifera* Robertson, new species**

(Pls. 53-57)

Range—Recent: known only from off northwestern Cuba, Greater Antilles, from the Virgin Islands, and from Antigua, Lesser Antilles. Presumably widespread around high islands throughout the West Indies, but very rarely collected.

Chief distinguishing characters—This is the only species in the genus having a shell with prominent spiral sculpture. This begins on the second whorl as keels, which soon become cords. On later whorls the cords are reduced and broadened to interspaces between sulci. These sulci are absent at and near the periphery of the last whorl of large shells. Also differs from other Recent species in the genus as follows: very fine axial threads on second whorl; color pattern with

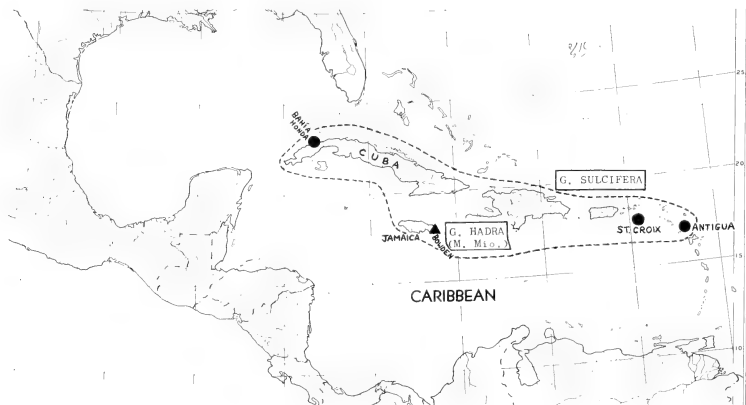


Plate 53. Geographical records of *Gabrielona sulcifera* Robertson (Recent) [round spots] and *Gabrielona hadra*

(Woodring), its Middle Miocene (or Plio-Pleistocene) precursor [triangle].

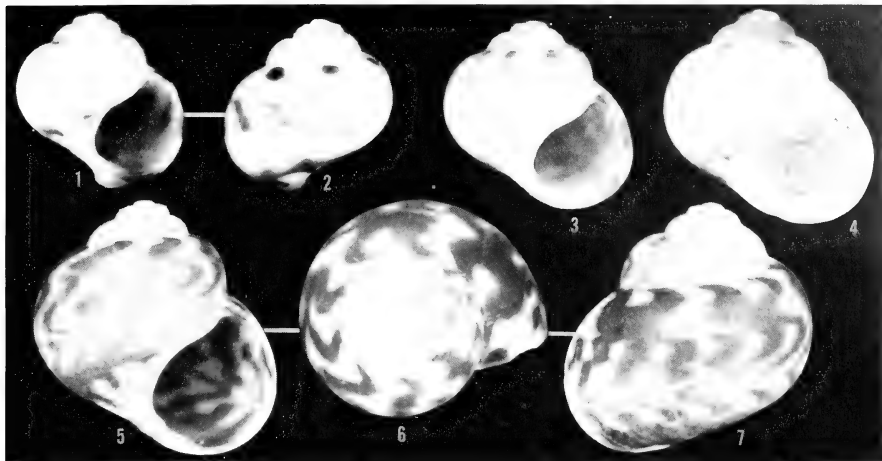


Plate 54. *Gabrielona sulcifera* Robertson. Antigua, Lesser Antilles. Fig. 4. Holotype. All x20.

no demarcated subsutural area; palatal sulcus near middle of aperture and not correlated with color pattern on external surface; palatal denticle can be present; only lower columellar denticle (cd_2) present (abnormally, slight trace upper columellar denticle); operculum with prominent spiral cord at inner edge marginal spiral ridge. For differences from *G. hadra*, see under that species.

Relationships—Judging by the presence and kind of sculpture (even though spiral and not axial), the fairly thick, generally similarly-shaped shells, and the two opercular resemblances, *G. sulcifera* seems more closely related to *G. raunana* than to the other two Recent species. However, the differences are far greater than those between *G. nepeanensis* and *G. pisinna*.

Abundance—14 specimens available, only 1 live-collected and with an operculum.

Habitat—The single live-collected specimen and 11 empty shells were all dredged together at an unrecorded depth at Antigua, and were in "deep, fine sand and shells." To have been in or near English Harbour, the depth must have been less than about 20 fathoms (H.O. chart 366). The empty, drilled, abnormal shell from 287 fathoms off northwestern Cuba probably was adventitious at that depth.

Shell description [*see also section on abnormal shell*].—Attains length of 2.4 mm., width

of 2.3 mm., and 4.3 whorls; spire angle 90° – 105° ; length exceeds width, and even small shells high-spired; outline fairly variable (Pl. 56, figs. 1–3); fairly thick and slightly translucent to slightly transparent. Protoconch slightly exsert, slightly inflated, smooth, white, fairly prominently demarcated from teleoconch by slight varix, 1.1–1.2 whorls. First whorl 0.25–0.26 mm. in diameter. Penultimate and last whorls: flattening below suture and slight shoulder (Pl. 56, figs. 1–3); commonly: slight spiral bulge around umbilical area (Pl. 56, figs. 4, 9). Sculpture of second whorl: 3 spiral keels on first quadrant following protoconch varix, the middle keel (on shoulder) the most prominent; keels less prominent on second to fourth quadrant, gradually becoming spiral cords, with one or two more cords intercalated; very fine axial threads (Pl. 56, fig. 5). On later whorls, cords are reduced and broadened to interspaces between spiral sulci; 8–12 sulci above suture on penultimate whorl. Last whorl of small shells: 25–28 spiral sulci between suture and base. Sulci absent at and near periphery of large shells, and wholly absent near outer lip where surface is smooth except for axial growth lines; sulci fairly regularly to irregularly spaced (fairly uncommonly, in closely-spaced pairs), especially variable below and near suture; termination of sulci commonly abrupt. Surface shiny. Colors: pale pinkish brown or orange-brown, and white. Patterns: no demarcated subsutural area; on middle whorls: irregular axial bars at shoulder (0–10 per whorl), and near and

above periphery (7-17 per whorl), developing into wavy bands; on last whorl large shells: axially aligned, broadly wavy brownish bands arising from suture and extending to base, 6-11 on last whorl, commonly coalesced into irregular spiral areas on shoulder and on base, and commonly disjunct subperipherally; umbilical area: white, with 5-9 (usually 6) axial or very steeply descending brownish bands extending from middle of base; fairly rarely: all brownish marks very pale and peripheral area uniformly whitish (Pl. 54, fig. 4). Aperture slightly more rounded than in other Recent species (less constricted near suture); outer lip and callus on upper parietal area fairly thick to thick; palatal denticle on most large shells, commonly wide and faint; apertural ridge (ar) shallow in aperture; palatal sulcus near middle of aperture (lacking in smallest shell); upper columellar denticle (cd₁) absent; lower columellar denticle (cd₂) present, commonly wide (Pl. 56, figs. 4, 9). Columellar lip not thickened, and steep slope into umbilical channel but no escarpment; escarpment to left of umbilical channel fairly prominent, arising fairly high to high off outer edge columellar lip; broad area to left of this escarpment, commonly with several parallel threads; umbilicus fairly wide to wide.

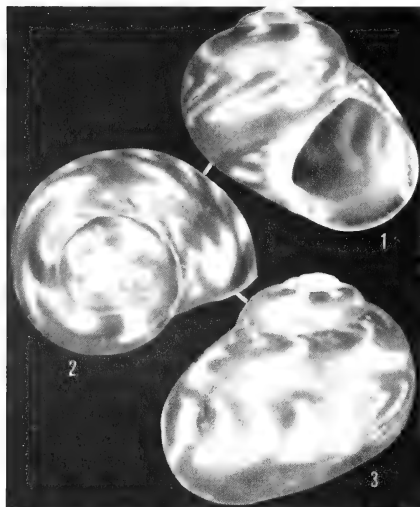


Plate 55. *Gabrielona sulcifera* Robertson. Off northwestern Cuba. Abnormal shell. All x20.

Abnormal shell (Pl. 55)—The single empty shell from 287 fathoms off northwestern Cuba (USNM no. 94974) differs strikingly from all those from Antigua, but seems to be conspecific. The protoconch and beginning of the second whorl are normal, but the surface is increasingly corroded as far as a growth line in the first quadrant of the third whorl. Thereafter, the external surface is smooth and shiny and lacks sulci. Another growth line is at the beginning of the second quadrant of the third whorl. I conclude from the growth-lines, which are much more clear-cut than on any other *Gabrielona* observed, that growth of this shell was abnormal, perhaps because the animal lived in an unusual habitat (depth?).

Other differences from the Antiguan specimens: spire lower (spire angle ca. 115°); width exceeds length (resembles *G. pisinna* in outline); thick; coloration dark brick red and white; dark areas large, with banding complex and greatly coalesced; apertural ridge (ar) fairly deep in aperture; slight trace upper columellar denticle (cd₁); shallow slope from columellar lip into wide umbilical channel; no trace escarpment to left.

Shell measurements (mm.)—

length	width	no. whorls	
2.42	2.27	4.3	largest (Antigua)
2.13	2.25	3.8	abnormal (N.W. Cuba)
1.98	1.93	4.0	average; holotype
1.33	1.17	3.5	smallest (St. Croix)

Operculum (Pl. 56, figs. 6-8)—The single operculum available is different from all other known *Gabrielona* opercula in having a prominent spiral cord at the inner edge of the marginal spiral ridge. The operculum of *G. sulcifera* is almost as thick as those of *G. raunana*, and the opercular whorl counts of these two species are also similar. In outline, the operculum of *G. sulcifera* is slightly more rounded than those of all the other Recent species—a consequence of the more rounded aperture. In the central region, a faint spiral ridge separates the smooth outer spiral area from the smooth central area. The callus is thin, revealing some of the spiral suture at the surface. The non-spiral columellar edge is steeply beveled. The spiral edge seems to be corroded at the external surface, and the sharp crest of the spiral ridge may therefore be an erosional feature.

Radula (Pl. 57; 1 studied)—Attains length of 0.7 mm., width of 0.13 mm., and with as many as 30

fairly strongly curved transverse rows of teeth (including a few nascent rows). Central monocuspid, with the small anterior portion of the base in a cleft between the bases of the innermost pair of laterals; the remainder of the base of the central overlapping these (where they are juxtaposed posteriorly). Five pairs of laterals, each of these (like the central) with a small distal portion that is monocuspid; the outer edge of each base partly overlaps the base lateral to it. As many as 34 pairs of marginals (lowest count 26), the innermost large and massive with lobed cusps, the distal portions gradually becoming smaller and more slender outwards, and with finer denticulations that finally are absent altogether on the outermost teeth.

Synonymy—

1889 *Phasianella (Eucosmia) brevis* "Orbigny" Dall [*Eucosmia brevis* in plate caption] (not *P. brevis* Orbigny, 1842). Bull. Mus. Comp. Zool. 18: 30 [listed], 351.

pl. 19, fig. 10b [not North Carolinian specimens, which are *Tricolia thalassicola* Robertson (deep water form) and perhaps other species of *Tricolia*].

1918 *Eucosmia brevis* ("Orbigny") Cossmann (not *P. brevis* Orbigny). Essais Paleconch. Comp., Paris, livr. 11, p. 162, fig. 55 [outline copied from Dall, 1889].

1958 *Gabrielona brevis* ("Orbigny") Robertson (not *P. brevis* Orbigny, 1842). Johnsonia 3 (37): 257-260, pl. 138, fig. 2 [radula], pl. 139, figs. 3-4 [operculum], pl. 140, figs. 2-3, pl. 141 [not pl. 142, fig. 1].

Types—The holotype (Pl. 54, fig. 4), the live-collected specimen from Antigua, is at the United States National Museum (no. 500636), Washington, D.C. Of the original 11 Antigua paratypes, 7 are still at USNM (no. 659066), 2 are at the Museum of Comparative Zoology (no. 188356), 1 is at the Academy of Natural Sciences of Philadelphia (no. 302625), and 1 (Pl. 54, fig. 3) was lost. The smallest paratype, from St. Croix, is in Mr. Usticke's private collection. The abnormal shell from Cuba is not a paratype.

Derivation of new name—Latin, *sulcifer*, bearing furrows.

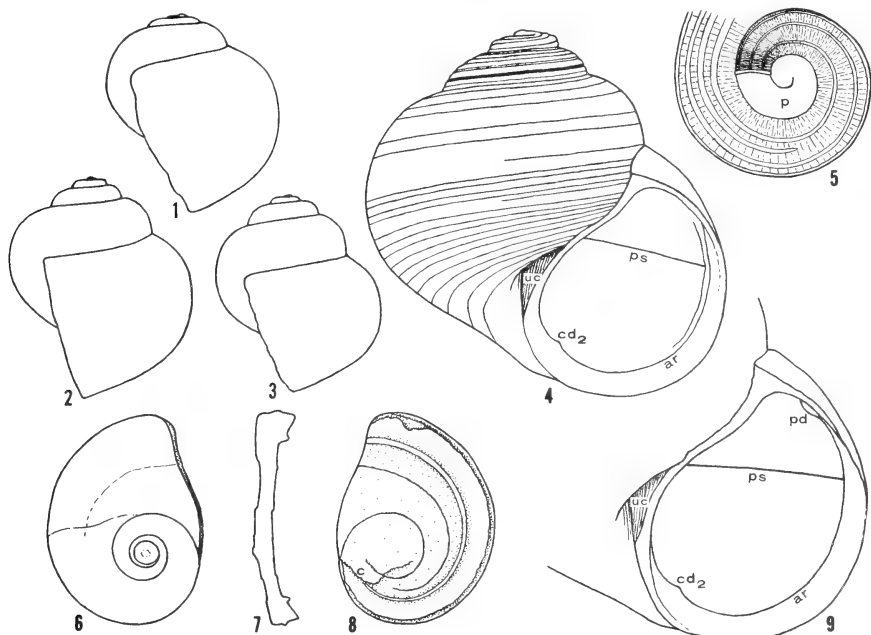


Plate 56. *Gabrielona sulcifera* Robertson. Figs. 1-3. Outlines of large shells, showing variation, all $\times 17$. Fig. 1. Abnormal shell from off northwestern Cuba. Fig. 3. Unusually high-spired shell. Fig. 4. Holotype, showing position of sulci, $\times 33$. Fig. 5. Apex, $\times 60$; p, protoconch. Figs. 6-8. Operculum of

holotype. Internal surface, longitudinal section, and external surface (respectively). All $\times 33$; c, lower edge of callus. Fig. 9. Aperture, $\times 33$; ar, apertural ridge; cd_2 , lower (inner) columellar denticle; pd, palatal denticle; ps, palatal sulcus; uc, umbilical channel.

Nomenclature—Following Dall (1889), who first applied the name *Phasianella brevis* Orbigny, 1842, to the abnormal Cuban shell discussed and refigured here (Pl. 55), I misapplied this name to this species and transferred it to *Gabrielona*. Subsequent study of the holotype (figured specimen) of *P. brevis* at the British Museum (Nat. Hist.), no. 1854.10.4.282, has shown that this is a depauperate *Tricolia*. This holotype, inadequately illustrated in Robertson (1958, pl. 142, fig. 1), will be treated in detail and refigured elsewhere.

Locality records (see map, Pl. 53, circular black spots)—CUBA: off Bahía Honda, Pinar del Río (23°2'N.; 83°13'W.; 287 fms.; Blake Sta. 21 [1877-78]; USNM). VIRGIN ISLANDS: Christiansted Harbor, St. Croix (dredged 15 ft [1 dead]; G. N. Ustick). LESSER ANTILLES: English Harbour, Antigua (1918, J. B. Henderson, Jr., USNM, MCZ, ANSP).

Erroneous locality record—Arenas de la Chorrera, Habana, Cuba (Robertson, 1958, pp. 259-260, as *G. brevis*) [a juvenile *Tricolia*].

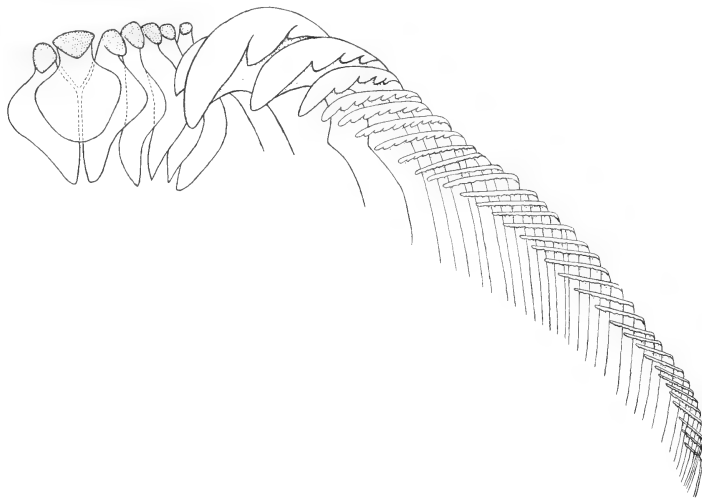


Plate 57. *Gabrielona sulcifera* Robertson. Half of one transverse row of radular teeth, showing (from left to right) the central between the innermost pair of laterals, the remaining four laterals on the right side, and the entire row of margin-

als. The cusps of the central and laterals are stippled. From the holotype, Antigua, West Indies. x1500. Modified from Robertson (1958, pl. 138, fig. 2, as *Gabrielona brevis*).

EXCLUDED SPECIES

"Gabrielona" brucasensis Weisbord, 1962

(Pl. 58)

Range—Upper Miocene or Pliocene (or younger?): known only from one locality in the Playa Grande Formation (Maiquetía Member), northern Venezuela.

Remarks—This species was described from a single poorly preserved shell with a badly broken columellar area. Even generic identification has been a problem but the shell does seem to be a phasianellid. However, it cannot be a *Gabrielona* because the slight axial ridge revealing the position of the withdrawn operculum is detectable, and this is fairly deep in the aperture. I detected no palatal sulcus or apertural denticles, and the part remaining of the umbilical area indicates that there was no *Gabrielona*-like umbilical channel. The outer lip is more prosocline than in any true *Gabrielona*. I conclude that *G. brucasensis* probably is a young *Tricolia*.

The specimen lacks most of the characters distinguishing species of *Tricolia*. The apex is in such poor condition that the whorls cannot be counted accurately and the first whorl cannot be measured. The shell is suffused with pale brownish pink, but no color pattern is detectable. Similar-sized shells of *T. affinis cruenta* Robertson differ in outline (are more elongate, with a more obtuse apex) and lack the umbilicus. *G. brucasensis* is here considered a *nomen dubium*.

Synonymy—

1962 *Gabrielona brucasensis* Weisbord, Bulls. American Paleol., 42(193): 111, pl. 8, figs. 5-7 (Quebrada las Bruscas [Playa Grande Formation], Distrito Federal, Venezuela).

Type—The holotype is at the Paleontological Research Institution (no. 26056), Ithaca, New York.

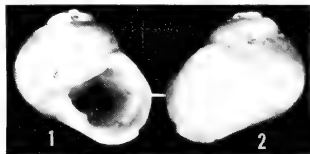


Plate 58. *"Gabrielona" brucasensis* Weisbord, probably a young *Tricolia*. Upper Miocene or Pliocene [?], northern Venezuela. Holotype. Both x20.

"Gabrielona" sphaera Weisbord, 1962

(Pl. 59)

Range—Pliocene (or younger?): known only from three nearby localities in the Mare Formation, northern Venezuela.

Remarks—This is a rissoacean. Although resembling in outline a high-spined *Gabrielona*, it cannot be one because the shell (for its size) is thin, the periphery of the last whorl is lower than in any known *Gabrielona*, the aperture is elongate-ovate, there are no apertural denticles, and neither is there a palatal sulcus. There is a wide umbilicus and a broad umbilical channel that is slightly angled at its lower left margin. The holotype has 3.4 whorls and the first whorl is 0.23 mm. in diameter. The callus on the upper parietal area is incomplete medially. In coloration, the shell is pale (faded?) amber and whitish near the umbilicus and on the last part of the last whorl where there are irregular amber markings. At the apex, the beginning of the suture is tinged with dark amber.

Synonymy—

1962 *Gabrielona sphaera* Weisbord, Bulls. American Paleol., 42(193): 109-111, pl. 8, figs. 1-4 (near Quebrada Mare Abajo [Mare Formation], Distrito Federal, Venezuela).

Types—The holotype is at the Paleontological Research Institution (no. 26054), Ithaca, New York. So also is the single paratype (no. 26055) distinguished by Weisbord among eleven other specimens identified with *G. sphaera*.



Plate 59. *"Gabrielona" sphaera* Weisbord, a rissoacean. Pliocene [?], northern Venezuela. Holotype. Both x20.

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trations of these morphological differences in Rosewater, 1970, and in this paper).

Most *Tectarius* s.s. and *Echininus* s.s. are living today only in the East Indian area. With the exception of *Tectarius grandinatus* whose range extends eastward to Polynesia, all other species are inhabitants of the raised, weathered coral reef shorelines found in the Western Pacific Arc (personal observations, 1970). It can only be assumed that this niche provides the requirements essential for the existence of these species as they are to be found nowhere else.

The fossil record provides very few clues to the origin of these groups. There are only three Tertiary fossil species described from the Indo-Pacific and these probably belong in three separate generic taxa. The oldest of these, *T. songoense* Martin, from the Upper Eocene of Java, probably represents nearly the earliest appearance of *Tectarius*. As mentioned in Part I, littorinid fossils are exceedingly difficult to separate from Trochidae and Turbinidae, and this is no less true for *Tectarius* and *Echininus*. Probably, however, these groups made their appearance in the early Tertiary within the region where they have developed, and with the exceptions of *Echininus* (*Tectininus*) *nodulosus* and *Tectarius* (*Cenchritis*) *muricatus*, both of the western Atlantic, they have remained there.

Opercula

The opercula of Indo-Pacific Littorinidae require special comment (see pl. 389). All are made up of conchiolin, and those of members of the subfamily Littorininae, including *Littorina*, its subgenera, and *Nodilittorina* are usually paucispiral and rather oval in shape with the nucleus at the side and nearer one end (oligogyrous spiral type of Fretter, et al., 1962, pp. 79,80). In the Echinininae, the basic plan of the operculum differs from that of other littorines. It is the type

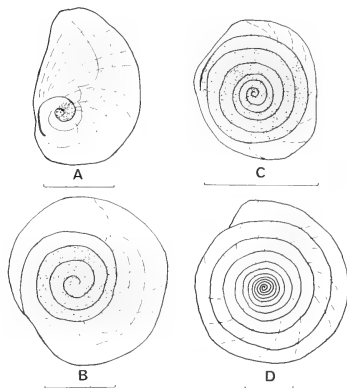


Plate 389. Opercula of Littorinidae and Trochidae.

Fig. A. Paucispiral operculum of *Littorina* (*Littorinopsis*) *scabra* (Linné) from Mokuoloe Id., Kaneohe Bay, Oahu (USNM 339388).

Fig. B. Mesospiral operculum of *Tectarius rusticus* (Philippi) from Troughton Chain, northern Western Australia (WAM 1787-69).

Fig. C. Multispiral operculum of *Echininus cumingi* (Philippi) from near Davao City, Mindanao, Philippines (WAM 1566-70).

Fig. D. Multispiral operculum of *Trochus niloticus* Linné, from Makuluva, Viti Levu, Fiji (USNM 531827).

Lines under each figure represent 5 mm.; stippled areas are thickened and dark-brown in color; non-stippled areas are light horn color and transparent.

of operculum which is called in other groups, such as Trochidae, a multispiral operculum (polygyrous spiral type of Fretter, et al., *ibid.*) although not so extreme as that figured by Fretter (*ibid.*, p. 80, fig. 43A; also see our pl. 389, fig. D.). The operculum is circular in outline and moderate to small in size. The nucleus is decidedly central in location and growth proceeds outward from the center in multiple, fairly evenly spaced gyrations (pl. 389, fig. D). The operculum in Tectariinae (fig. B) is intermediate in form between

Explanation to plate 388 (opposite page)

Figs. 1,2. *Tectarius grandinatus* (Gmelin) from Palmerston Atoll, Cook Islands (USNM 685165).

Figs. 3,4. *Tectarius tectumpersicum* (Linné). Fig. 3, from Stirling Isle, Treasury Ids., Solomon Islands (USNM 600370); Fig. 4, from "East Indies" (USNM 131450).

Figs. 5-7. *Tectarius pagodus* (Linné). Fig. 5, from "East Indies" (USNM 18966); Fig. 6, from the Philippines (USNM); Fig. 7, a young specimen from Polillo, Philippines (USNM 311141).

Figs. 8,9. *Tectarius rusticus* (Philippi) from Buccaneer Archipelago, Western Australia (USNM 684713).

Figs. 10,11 *Tectarius coronatus* Val. Fig. 10, from Pacific (USNM 304587); Fig. 11, from Davao Bay, Mindanao, Philippines (USNM 654034).

Figs. 12,13. *Echininus cumingi cumingi* (Philippi) from Hervey Ids., Cook Ids. (USNM 42452).

Figs. 14,15. *Echininus cumingi spinulosus* (Philippi) from Kadena Circle, Okinawa, Ryukyu Ids. (USNM 664658).

Figs. 16,17. *Tectarius* (*Cenchritis*) *muricatus* (Linné), from Boca de Camarioea, Matanzas, Cuba (USNM 599944).

Figs. 18-20. *Echininus* (*Tectininus*) *nodulosus* (Pfeiffer). Fig. 18, from Hog Island, Bahamas (USNM 603911); Figs. 19,20, from Mujeres Harbor, Quintana Roo, Mexico (USNM 662308).

Littorininae and Echinininae, being large and rather rounded in outline, with a slightly acentric nucleus and having a number of gyrations more than the paucispiral type but less in number than the multispiral type. The Tectariine opercular type is here termed the mesospiral or mesogyrous spiral type. The presence of the three opercular types in Littorinidae may be considered to have evolutionary significance, and possibly is related to selection for a better aperture sealing mechanism in animals which have considerable vertical distribution on the shore line: in order, proceeding from low toward higher shore habitats—Littorininae, Tectariinae, Echinininae.

Reproduction

To my knowledge nothing is known concerning reproduction in either Tectariinae or Echinininae with the exception of *Tectarius* (*Cenchritis*) *muricatus* (Linné) which produces a pelagic capsule (see Lebour, 1945, and Lewis, 1960, references in Rosewater, 1970 p. 05–276). Field and laboratory studies are needed to discover details of the life histories of the remaining species. However it is likely that most of these snails also produce eggs encased in pelagic capsules which undergo development in the sea. Abbott (1954) noted that Lebour (*ibid.*) stated that some of the Bermuda littorinids that live above high tide line migrate to the water to spawn. It is suspected that this also is the case with many of the Indo-Pacific species.

Acknowledgments

The persons and institutions acknowledged in Part I of this study (see Rosewater, Indo-Pacific Mollusca, vol. 2, no. 11, p. 425) also are thanked here. In addition, I acknowledge the following for their help in making possible the examination in the field of most of the species of *Tectarius* and *Echininus* during the National Geographic Society—Mariel King Memorial Expedition to the Moluccas Islands, Indonesia, May to July 1970: the late Mariel King, Mrs. Grace King, T. H. Richert, C. Beal, C. M. Burgess, B. R. Wilson, and the National Geographic Society. The Government of Indonesia graciously provided clearance for the vessel *Pele* to work in the Moluccas Islands. Mr. Kasim Moosa and Mr. Sukarno, both of the Institute for Marine Research, Djakarta, accompanied the expedition and provided assistance of many kinds.

List of Recognized Taxa

Below is a list of the Tertiary fossil and Recent species herein recognized as belonging in the subfamilies Tectariinae and Echinininae. The few fossil taxa are preceded by a dagger [†].

Family Littorinidae Gray, 1840

Subfamily Tectariinae, *new subfamily*

GENUS *Tectarius* Valenciennes, [1832]

Subgenus *Tectarius* Valenciennes, [1832]

coronatus Val., 1832. **Type.** Recent, western Pacific ★

grandinatus (Gmelin, 1791). Recent, Pacific islands

pagodus (Linné, 1758). Recent, western Pacific

tectumpersicum (Linné, 1758). Recent, western Pacific

rusticus (Philippi, 1846). Recent, northern Australia

†*songocense* (K. Martin, 1931). Eocene, Java.

Subgenus

†*Subditotectarius* Ladd, 1966

trehderi Ladd, 1966. **Type.** Miocene, Marshall Islands.

Subgenus *Cenchritis* von Martens, 1900

muricatus (Linne, 1758). **Type.** Recent, tropical western Atlantic.

Subfamily Echinininae, *new subfamily*

GENUS *Echininus* Clench and Abbott, 1942

Subgenus *Echininus* Clench and Abbott, 1942

cumingi cumingi (Philippi, 1846). **Type.** Recent, western Pacific

cumingi spinulosus (Philippi, 1847). Recent, western Pacific

†*adelaidensis* (Cotton, 1947). Pliocene, South Australia.

Subgenus *Tectininus* Clench and Abbott, 1942

nodulosus (Pfeiffer, 1839). **Type.** Recent, tropical western Atlantic.

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Key to the Tectariinae and Echinininae

The following key is to the genera and subgenera of these two subfamilies. It is based upon the shell and externally observable characters. Page numbers are given for Indo-Pacific groups

only, since Western Atlantic taxa are not treated in detail in the present paper. For a key to the Littorininae, see vol. 2, no. 11, p. 430 [p. 05-278].

- 1a Shell umbilicate 2
 1b Shell not umbilicate 3
- 2a Shell spinose, with partially open spines, shell about as wide as high, operculum multispiral (see pl 389) *Echininus* p. 526
 2b Shell not spinose, nodulose, higher than wide, operculum not multispiral *Cenchritis*
- 3a Shell spinose, operculum mesospiral. *Tectarius* p. 513
 3b Shell nodulose, fossil *Subditotectarius* p. 524
 3c Shell moderately spinose, operculum multispiral *Tectininus*

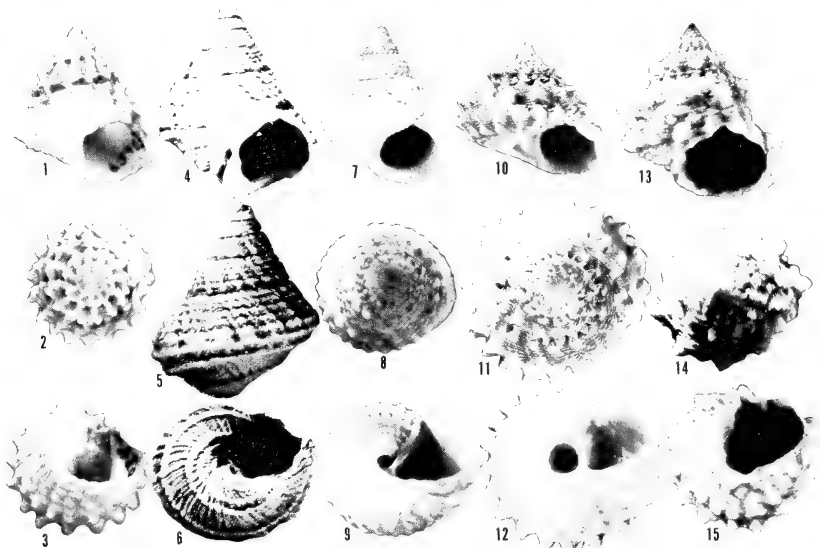


Plate 390. Type-species of Genera and Subgenera of Tectariinae (Figs. 1-9) and Echinininae (Figs. 10-15) illustrating sculpture, arrangement of spines, and presence or absence of umbilici.

- ★ Figs. 1-3. *Tectarius* (*Tectarius*) *coronatus* Val.; Davao Bay, Mindanao, Philippines (USNM 654034; 23.1 × 17.8 mm.).
 Figs. 4-6. *Tectarius* (*Subditotectarius*) *rehderi* Ladd; early

Miocene, Marshall Islands (Holotype, USNM 648342; 2.8 × 2.4 mm.).

Figs. 7-9. *Tectarius* (*Cenchritis*) *muricatus* (Linné); Matanzas, Cuba (USNM 599944; 26.1 × 17.9 mm.).

Figs. 10-12. *Echininus* (*Echininus*) *cumingi* (Philippi); Cook Islands (USNM 42452a; 17.2 × 17.5 mm.).

Figs. 13-15. *Echininus* (*Tectininus*) *nodulosus* (Pfeiffer); Cozumel Id., Mexico (USNM 662806; 14.4 × 12.2 mm.).

Subfamily Tectariinae, new subfamily

Genus Tectarius Valenciennes, [1832]

Type: *Tectarius coronatus* Val., 1832

The genus *Tectarius sensu lato* includes the nominate subgenus, *Tectarius*, whose type-species *T. coronatus* Val. (= *T. papillosus* 'Lamarck' of authors) has one of the more conservatively sculptured shells of the group. *Tectarius sensu stricto* is a wholly Indo-Pacific group, having its present population center in the Western Pacific Arc. The monotypic subgenus *Cenchritis* von Martens contains only *T. (C.) muricatus* (Linné), of the tropical western Atlantic (see pl. 388, figs. 16, 17). *Subditotectarius* Ladd, 1966, is monotypic for the fossil *T. (S.) rehderi* Ladd, of the Miocene of the Marshall Islands. Only species belonging to *Tectarius* s.s. and *Subditotectarius* will be considered here.

Tectarius appears more closely related to *Littorina* than to *Echininus* because of greater similarities in morphology, general shell characters, the absence of a truly multispiral operculum, a broader, less modified central radula tooth, and the usual lack of an openly umbilicate shell.

Subgenus Tectarius sensu stricto

Moderately large, pyramidal to turbanate, non-umbilicate littorinids with from rather strongly spinose to nodulose or papillose shells; generally living at or above high tide line. Radula littorinoid, the central tooth somewhat narrowed, the lateral tooth with an embayment and usually developing a medial vertical ridge or partition. In males the penis is large and well-supplied with glands along most of its lateral edge, the remainder papillose, and with an open but deeply folded seminal duct. Operculum rounded, mesospiral (see *Opercula* in Introduction). Aperture plicate within; with a columellar swelling or tooth.

Synonymy—

- 1798 *Cidar* Röding, Museum Boltenianum, part 2, p. 84; type-species by subsequent designation, Hermannsen, 1847: *Trochus pagodus* Linné; non *Cidar* Leske, 1778, nor Swainson, 1840.

- [1832] *Tectarius* Valenciennes, *Coquilles*, in Humboldt and Bonpland. Voyage aux régions équinoxiales du Nouveau Continent, Observations de Zoologie, vol. 2, p. 271; type-species by subsequent designation Clench and Abbott, 1942: *Trochus coronatus* Valenciennes. ★
- 1839 *Pagodus* Gray, in *Molluscosus Animals: The Zoology of Captain Beechey's Voyage*, p. 141; type-species by Monotypy and by absolute tautonymy, *Monodonta pagodus* Lamarck [= *Tectarius pagodus* (Linné)].
- 1840 *Pagodella* Swainson, A Treatise on Malacology, pp. 207, 219, 221 [refers to *Pagodella echinata*, nomen nudum] 351; refers to *P. major* Martini - Chemnitz, pl. 163, figs 1541, 1542 [= *Tectarius pagodus* (Linné)] and to *T. tectumpersicum* ibid., fig. 1543, 1544; type-species here designated: *Tectarius pagodus* (Linné).
- 1840 *Echinella* Swainson, ibid., pp. 207, 221, 352; refers to *E. granulata* Swainson [nomen nudum] and to *E. coronaria*, Tableau Encyclopedique et Methodique, pl. 447, fig 6 [= *Mondonta coronaria* Lamarck = *Tectarius grandinatus* (Gmelin)]; type-species by monotypy, *Tectarius grandinatus* (Gmelin) [also see Clench and Abbott, 1942]; not *Echinella* Bory St. Vincent, 1824.
- 1846 *Fectaria* Philippi, Abbildungen und Beschreibungen Conchylien, Vol. 2, *Littorina*, p. 139; used in combination *Fectaria pagodus*; error for *Tectarius valenciennesi*.
- 1858 *Hamus* 'Klein' H. & A. Adams, The Genera of Recent Mollusca, vol. 2, p. 656, refers to H. & A. Adams, 1854, vol. 1, p. 315; type-species here designated, *Hamus pagodus* (Linné) [= *Tectarius pagodus* (Linné)]; not *Hamus* 'Klein' R. B. Watson, 1886 [= *Trochidae*].
- 1899 *Echinellopsis* Rovereto, Atti della Società Ligustica di Scienze naturali e geografiche, vol. 10, p. 109; new name for *Echinella* Swainson, 1840, not Bory St. Vincent, 1824.

Nomenclature—Due to similarities between the shells of *Tectarius* and some of the Trochidae, there has been a tendency for some of the former to be classified with the latter. This problem was discussed by Keen (1966) who recommended that the International Commission on Zoological Nomenclature validate *Tectarius* with the type-species *Tectarius coronatus* Valenciennes, [1832], i.e., in its accustomed sense. Her petition was granted in I.C.Z.N. Opinion 871 (Melville and China, 1969). It was assumed in this Opinion that the type-species of *Tectarius*, *T. coronatus* Valenciennes, is a synonym of *T. grandinatus* Gmelin. However, these are in actuality distinct and geographically isolated species. ★

Another name which sometimes has been associated with *Tectarius* that has an exceedingly long and complicated history is the genus *Hamus*. It was mentioned originally by Klein (1753) where its use was of course pre-linnaean. Bruguière (1792) gave a brief description, referring to Klein, but listed no species. Deshayes (1830)

declared it "a forgotten genus", indicating that he considered it unrecognizable. Mörch (1852) listed it, this time in the synonymy of *Littorina* Férussac, an invalid introduction (I.C.Z.N., Art. 11(d)). The first valid use of *Hamus* was not until H. & A. Adams (1858) used it as a senior synonym for *Tectarius* (see synonymy). It was later used by Wimmer (1880) and Watson (1886), the last being a taxon of Trochidae. I have designated as type-species of *Hamus* H. and A. Adams, 1858, *H. pagodus* (Linné) and consider this genus to be an absolute synonym of *Tectarius* Valenciennes.

The use of square brackets surrounding the date for *Tectarius* Valenciennes, [1832] is recommended by the International Code of Zoological Nomenclature in cases where the date of publication of a name has been determined on the basis of external evidence (I.C.Z.N. Recommendation 22A(3); also see Sherborn and Woodward, 1901; Keen, 1966; and Opinion 871).

★ *Tectarius coronatus* Valenciennes, 1832

(Pl. 388, figs. 10, 11)

Range—Philippines and Indonesia.

- Remarks—The shells of well prepared and cleaned specimens of *Tectarius coronatus* tend to be quite colorful for Littorinidae, with the orange-pink coloration of the last two whorls contrasting with a purplish brown subsutural band. These colors do not show well in all specimens, however, and are not very visible in uncleaned specimens. The three large, non-umbilicate common species of the southwest Pacific may be distinguished by the number of major spiral rows of spines on the last whorl: 2 in *pagodus*; 3 in *tectumpersicum*; and 4 in *coronatus*.
- ★ The closely-spaced stubby spines of *coronatus* also separate it from the other two. These characteristics do not of course help to distinguish it from *T. grandinatus*, but other characters and the Polynesian endemicity of the latter are helpful in this case (see *Remarks* under *grandinatus*).

Habitat—Shore rocks and limestone cliffs 1-2 meters above high tide line (personal observations, Davao, Philippines, 1970).

Description—Shell reaching 39.7 mm (about 1½ inches) in length, broadly conical in shape, average obesity about .76 (51 specimens range from .68-.82); mature specimens moderately heavily constructed, imperforate, and sculptured on most postnuclear whorls with four, fairly closely-spaced rows of stubby, rounded, often slightly upturned spines. External color generally

yellowish white on early whorls, becoming pinkish orange on penultimate and body whorls; area of most posterior (subsutural) row of spines usually a contrasting purplish brown, and the same dark color may appear in lines and dashes inside outer lip of aperture; aperture tinted lighter pinkish orange. Base flattened, sculptured spirally with nodulose cords, a larger separate row just below periphery of body whorl. Whorls 6-8, flat-sided excepting spines. Length of spire usually greater than half the length of shell. Spire convex, produced at an angle of from about 60-67°. Aperture rounded-squarish; outer lip thickly produced in mature individuals, strongly plicate within; plicae not reaching edge of aperture; outer lip tapering to a thin, crenulate edge; inner lip smooth posteriorly, often stained a deeper orange than rest of aperture, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture obscured by anteriormost row of spines of preceding whorl. Primary sculptural feature is the four spiral rows of spines. Spines not particularly aligned axially, although anteriormost 2 rows more so than others; from 17-23 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae. Posteriormost-but-one (3rd) row of

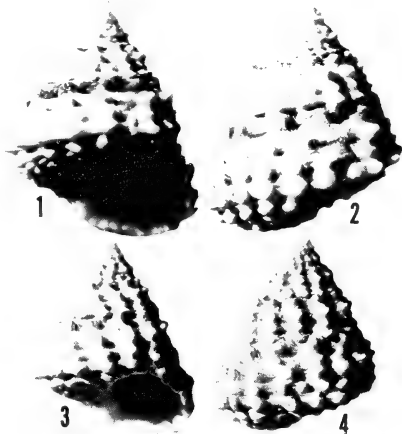


Plate 391. *Tectarius coronatus*

★
Figs. 1, 2. *Turbo rugosus* Wood, lectotype, BM(NH) 1968370, 28.4 × 22.3 mm.

Figs. 3, 4. *Tectarius coronatus* Valenciennes, Holotype, MHNP ("Acapulco") [Luzon, Philippines] 32.9 × 25.7 mm.

spines protrudes farthest on spire whorls, but this distinction largely lost on more mature whorls; posteriormost (4th) row of spines obscured by subapical purplish brown color band especially on penultimate and body whorls. Secondary spiral sculpture, between each row of spines, consisting of raised cords, and overall spiral sculpture of microscopic threads. Axial sculpture consists of irregular flaky lines of growth. Operculum moderate in size, circular, an average one measuring about 7 mm. in diameter, thin, light-brown with a dark-brown center, paucispiral, nucleus about central. Periostracum not evident. Nuclear whorls at least partially decollate in all specimens examined, about 2, smooth, grayish white, first postnuclear whorls showing early signs of spiral striae and becoming nodulose. Radula littorinoid, 2-1-1-1-2; lateral tooth with a vertical partition and an embayment typical of Littorinidae. Animal moderately large, littorinoid; penis large, muscular and apparently highly extensible; seminal groove in deep fold running along medial edge to tip; tip vermiform, covered with papillae; lateral edge of penis supplied with large number of glands not extending onto vermiform tip. Reproductive data and life history unknown.

Measurements (mm) (all Philippines)—

length	width	No. whorls	locality
39.7	27.6	7+	Cadao Id., Naro Bay, Masbate
35.4	25.2	7+	Cadao Id., Naro Bay, Masbate
30.1	22.4	7+	San Miguel Bay, Ticao
25.9	21.2	8	Batag Id., Samar
23.9	16.3	7+	Bongao Channel, SW Sanga Sanga Id., Sulu Archipelago
21.0	15.3	7+	Borongan, E side Samar
17.5	13.7	7+	Papahag Id., Tawi Tawi Group
15.0	12.0	6+	Borongan Village, E side Samar
13.5	10.8	7+	Papahag Id., Tawi Tawi Group
12.6	9.8	6+	Papahag Id., Tawi Tawi
11.2	8.4	6+	Papahag Id., Tawi Tawi
8.4	6.8	5+	Papahag Id., Tawi Tawi

Synonymy—

— *Monodonta papillosa* of authors, not *M. papillosa* Lamarck, 1822 [= *Tectarius tectumpersicum* (Linne, 1758)].

1828 *Trochus rugosus* Wood, Supplement to the Index Testaceologicus or a Catalogue of Shells, British and Foreign, pl. 5, *Trochus*, fig. 7 (no locality given; Mindanao, Philippines, here selected); lectotype in BM(NH) 1968370, length 28.4 mm, width (ca.) 22.3; not *Litorina rugosa* Menke, 1843 [= *Nodilittorina australis* (Gray, 1926)]. Not Röding, 1798; Brown, 1818.

★ 1832 *Tectarius coronatus* Valenciennes in Humboldt and Bonpland, Voyage aux régions équinoxiales du Nouveau Continent, vol. 2, *Coquilles*, p. 271 (Acapulco [in error] locality here corrected to Luzon, Philippines); Holotype in MHNP.

1846 *Litorina papillosa elegans* Philippi, Abbildungen und Beschreibungen Conchylien, vol. 2, p. 140, *Litorina*, pl. 2, figs. 5, 7 (precise locality not given); figured specimens from Cuming Collection BM(NH) [not seen during 1968 visit] and Saul Collection, Cambridge Museum.

1846 *Litorina papillosa quadriseriata* Philippi, *ibid.*, p. 140, *Litorina*, pl. 2, fig. 2 (Zanzibar [in error] locality here corrected to Luzon, Philippines); type-specimen may be in BM(NH) [not seen during 1968 visit]; refers to "*Trochus rugosus* Wood Suppl. t.5, f. 7".

Types—Although the name *T. papillosus* has been applied to this species (see Kaicher, 1956) the type-specimen of that species in the Geneva Museum is unquestionably *T. tectumpersicum* Linné, and *papillosus* is, therefore an absolute synonym of *tectumpersicum* (q.v.). It also has been referred to as *Echinellopsis grandinatus* (Habe, 1961, p. 20; 1964, p. 28, both pl. 9, fig. 30) which is an error of nomenclature for *T. rugosus*. The first available name is *Tectarius coronatus* Val. [1832], the holotype of which is in the Paris Museum. The figured specimens of Philippi's *elegans* and *quadriseriata* may be in the BM (NH) and/or the Cambridge Museum. They were not discovered by me at the BM and may be lost. Philippi's figures are quite adequate for the interpretation of the species and may be considered as representative of the lectotypes: *elegans*, pl. 2, fig. 7; *quadriseriata*, pl. 2, fig. 2.

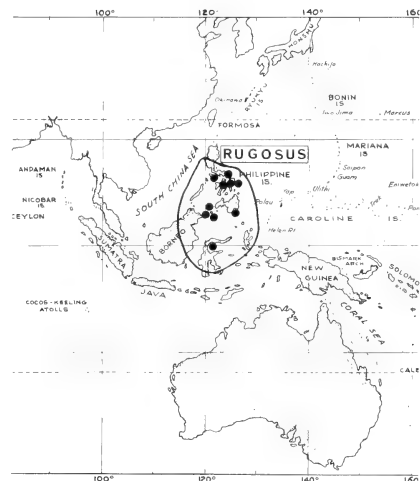


Plate 392. Geographic distribution of *Tectarius coronatus* (Wood) in the Philippines and Indonesia.

Records—PHILIPPINES: Port Galera, Mindoro; San Miguel Bay, Ticao Id.; Caddao Id., Naro Bay, Masbate (all USNM); Borongan Village (USNM, Del. Mus. N.H., ANSP, MCZ); Batag Id., both Samar (USNM); Samal Id., Davao Bay (MCZ, USNM, WAM); Zamboanga, both Mindanao (ANSP, Del. Mus. N.H.); Jolo Id. (MCZ); Tabawan Id. (ANSP); Papahag Id. (USNM); Bongao Channel, SW Sanga Sanga Id., all Sulu Archipelago (ANSP). INDONESIA: Buka Buka Id., Gulf of Tomini, Celebes (USNM).

***Tectarius grandinatus* (Gmelin, 1791)**

(Pl. 388, figs. 1,2; pls. 393-395)

Range—The Cook, Society, Tuamotu and Gambier Islands, southeastern Polynesia.

Remarks—*Tectarius grandinatus*, an inhabitant of southeastern Polynesia, apparently is geographically isolated from the several other members of the genus *Tectarius* in the Indo-Pacific, the others being found in the East Indies. It is quite distinct, morphologically, from *pagodus* and *tectumpersicum*, but, interestingly, is very close in appearance to *T. coronatus* in general matters of sculpture and external anatomy of the animal. Superficially, *grandinatus* might be thought more closely related to *Cenchritis muricatus* (L.) of the western Atlantic. However, the radula, penial anatomy (Abbott, 1954) and a close examination of shell sculpture and structure causes me to reject that theory: *grandinatus* has not been observed to be umbilicate, while *muricatus* sometimes is; the aperture of *muricatus* is never thickened and plicate as it is in *grandinatus*; the operculum of *grandinatus* is rounded with the nucleus near the center, that of *muricatus* is more oval with the nucleus near the side.

★ The many similarities between *coronatus* and *grandinatus* together with their spatial isolation suggest the possibility that they may have evolved from the same species stock. Although a subspecific relationship may be indicated, the two are here considered to have developed full specific differentiation.

Habitat—Usually occurs on low islands within the geographic range; on coral reef flats near the high tide line, on jagged pieces of raised reef.

Description—Shell reaching 37.9 mm (about 1 1/2 inches) in length, elongate conical in shape, average obesity about .72 (44 specimens range from .62–.82); rather solidly and thickly constructed for its size, imperforate; mature specimens with very deeply impressed suture and rounded whorls; sculptured with four spiral rows per whorl of stubby spines. External shell color yellowish white; often coated with what appears

to be a light-yellow to brown or rather dark grayish brown periostracum which may wear thin especially at tips of spines; no definite color pattern apparent; occasional lines or splotches of medium brown present; upper (most posterior) part of aperture usually covered with a brown glaze. Base moderately flattened, sculptured spirally with nodulose cords. Whorls 7-9, moderately rounded. Length of spire usually considerably greater than half the length of shell. Spire convex, produced at an angle of from 58-60°. Aperture rounded; outer lip considerably thickened, plicate within, tapering to a thinner, crenulate edge. Inner lip with a thin, brown glaze posteriorly, forming a tooth-like bulge anteriorly, near junction with outer lip near base of columella. Suture often deeply impressed, typically forming a channel between whorls. Primary sculptural feature is the four spiral rows of spines. Spines not regularly aligned axially, although anteriormost two rows more-so than others; from about 17-25 spines per row on body whorl; bases of anteriormost 3 rows of spines joined by low spiral carinae; bases of posteriormost row of spines usually separate; second from anterior row usually the smallest. Secondary spiral sculpture be-

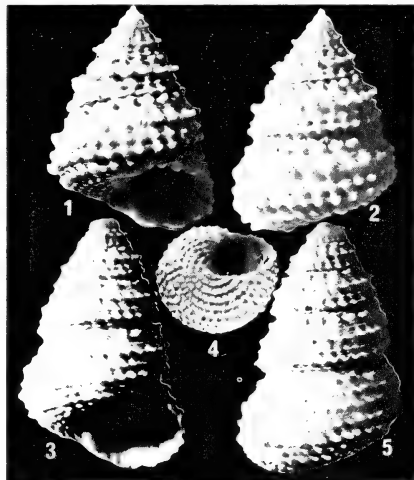


Plate 393. *Tectarius grandinatus* (Gmelin, 1791).

Figs. 1,2. *Trochus grandinatus* Gmelin, lectotype in ZMC, specimen figured by Chemnitz, Conchylien Cabinet, vol. 10, pl. 169, fig. 1639, from Palmerston Atoll, Cook Islands, 32 × 22.4 mm.

Figs. 3-5. *Monodonta coronaria* Lamarck, holotype, MHNG 1096/23, 41 × 27 mm.

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Auckland Institute and Museum
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Introduction

This monograph deals with the Patellidae, one of the five families of limpets that comprise the superfamily Patelloacea. The patellid limpets are of littoral and shallow-water occurrence and although widely distributed, cannot be considered cosmopolitan, since they are absent from certain extensive areas, namely, both coasts of North America, the Caribbean, and South America, north of Chile and Patagonia.

Although this work is concerned primarily with the Indo-Pacific fauna, it is deemed necessary to extend the scope to world coverage in order to explain the otherwise apparently anomalous distributional patterns.

A complication is encountered with the deceptively similar shells of an allied family, the Acmaeidae, members of which are easily separable from the Patellidae upon anatomical grounds, but the shell of which usually has no character that can be considered consistently diagnostic; hence, with fossil limpets there is often an element of doubt regarding family allocation.

Where patellids are absent, notably along the North West American coast, the acmaeids take over the corresponding littoral, ecological niche, and in so doing, attain shell sizes very large for acmaeids, which usually are of relatively smaller size than patellids. A striking instance of gigantism is the Californian *Lottia gigantea* Gray, 1834, which may reach a length of four inches.

Limpets tend to vary greatly in size, shape, sculpture and colour pattern, due to the ecological factors involved, particularly the relative exposure to wave stress and the nature of the substratum. Often, specific limits are apparent only when extensive series from a number of stations are studied.

Limpets featured frequently in early conchological works, but many of the species named are difficult to determine with accuracy, since, for the most part, they were based upon crude figures, inadequate descriptions, and with uncertain locality data.

Under the heading of "Species no longer included in the Patellidae" (pp. 84 to 87) 259

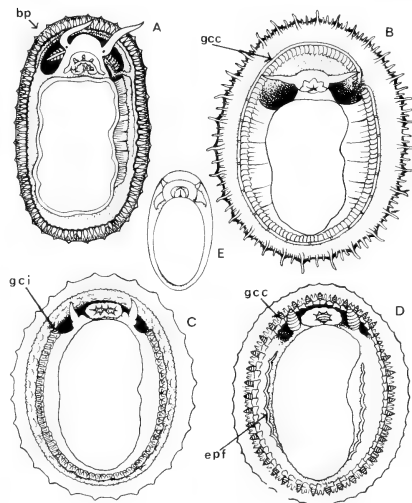


Plate 60. Gill structures in the Acmaeidae, Patellidae and Lepetidae.

A = *Acmaea virginea* (Müller); bp = branchial plume, behind head.

B = *Patella vulgata* Linnaeus; gcc = gill cordon, complete.

C = *Cellana radians* (Gmelin); gci = gill cordon, interrupted over head area.

D = *Nacella (Patinigera) terroris* (Filhol); gcc = gill cordon complete; epf = epipodial fringe (only in *Nacella* and *Patinigera*).

E = *Lepeta coppingeri* (E. A. Smith); no gills; respiration by means of cilia-lined pallial groove.

(Fig. A from Fretter and Graham, 1962, p. 120, fig. 73. Fig. E from Eales, 1923, p. 6, fig. 3).

species, described as *Patella* are listed, and their present familial location indicated. This list includes species now known to belong to the Acmaeidae, Lepetidae, Phenacolepatidae, Cocculinidae, Fissurellidae, Stomatellidae, Calyptraeidae, Capulidae, Hipponicidae, Muricidae, Trimusculidae, Siphonariidae, Umbraculidae, Ancyliidae, and even one considered to be based upon one of the accessory plates of a member of the Pholadidae.

Family Patellidae Rafinesque, 1815

The family Patellidae is one of three widespread families—the Acmaeidae Carpenter, 1857, the Patellidae Rafinesque, 1815, and the Lepetidae Dall, 1869, all belonging to the superfamily Patellacea.

Two other families, consisting of fossil species only, are placed provisionally in the Patellacea; they are the Metoptomatidae Wenz, 1938, of the middle Silurian to middle Permian, and the Symmetrocipulidae Wenz, 1938, of the Triassic, Jurassic and possibly Cretaceous.

The limpet shell is a simple shield or cap-shaped structure, and is unfortunately a shell-form that is simulated by molluscs belonging to several other gastropod orders. The one most frequently mistaken for a patellid limpet is *Siphonaria*, a member of the air-breathing pulmonates, being almost at the top rung of the gastropod ladder of evolution, whereas the Patellacea are located down towards the foot of the ladder. In between are the fissurellids, crepidulids, capulids and umbraculids, all of which have certain members that have limpetlike shells.

Limpetlike shells have developed independently in direct response to ecological necessity, being the shell-form affording the greatest amount of suction area for clinging to a rock surface, coupled with a low profile to withstand wave stress.

Classification of the patellid limpets, therefore, is dependent upon some knowledge of the animal. Even the allocation of species to either the Acmaeidae or the Patellidae, the two major families of the Patellacea, in many instances becomes conjectural upon the evidence from the shell alone.

Anatomical Outline of the Families and Major Genera of the Patellacea

Family Acmaeidae

- A Leaf-shaped ctenidium only *Acmaea*
 B Ctenidium present, plus gill cordon.
 Radula; closely spaced pair of centrals alternating with wider spaced pair of laterals; marginals vestigial or absent.
 Gill cordon complete *Scurria*
 Gill cordon interrupted by head *Lottia*

Family Patellidae

- C Ctenidium absent; replaced by gill cordon.
 Radula; 4 or 5 central teeth, median one present, vestigial or absent; lateral large, pluricuspid; marginals 3, weak or vestigial.
 Gill cordon complete *Patella*
 Radula; median central vestigial or absent; alternate pairs of long curved centrals and laterals; marginals 3, weak to vestigial.
 Gill cordon interrupted by head.
 Epipodial fringe absent *Cellana*
 Gill cordon complete.
 Epipodial fringe present *Nacella*; *Patinigera*

Family Lepetidae

- D No gills; respiration by cilia-lined pallial groove.
 Radula; large central, with prominent dentate cusp; no laterals;
 2 functional marginals *Lepeta*

Biology

The embryo of *Patella* hatches 24 hours after fertilization. The trochophore is about 0.18 mm. in diameter, with a tuft of erect apical cilia and two rows of ciliated cells around the greatest perimeter of the larva. The cilia beat in clockwise manner and rotate the top-shaped larva through the water. Two days after fertilization the larva is transformed into a pretorsional veliger, and both shell and foot appear. Torsion then begins while the larva is free-swimming. During the next stage of about 30 hours the larva both swims and crawls, and torsion is completed when the larva is $3\frac{1}{2}$ to 4 days old, and this marks the end of its pelagic life. The velum does not disappear until the snail has been actively crawling for about the third week. About this time the operculum is lost. The shell of the veliger is a dextral coil of scarcely one whorl, and this is soon replaced by a new shell, after which the limpet's post-larval life continues into the adult. (see Fretter and Graham, 1962, pp. 448-450 for a more detailed account).

The English *Patella vulgata* is a protandrous hermaphrodite with most, if not all, individuals starting life as male but later changing to female at the age of one year or more. Investigations of English populations of *vulgata* have shown that 90% of the limpets between 16 and 25 mm. in length are male; in those about 40 mm. in length the sexes are about equal; and in those 60 mm. or more in length most are female (see Fretter and Graham, 1962, p. 372).

Most patellids feed upon small species of living algae, but some live upon giant kelp, where they scrape away the surface tissue. The rock-dwelling patellids feed with the head end moving methodically from side to side, while the radula operates like a scythe. Patellids often travel up to four or five feet in search of food, and usually manage to return to their original resting places. This sometimes involves re-finding a site previously excavated in the rock that exactly fits the indentations of the shell margin. When rock faces have a slight coating of silt, limpet journeys can be seen quite plainly, and possibly the limpet uses its outward track in finding its way home.

The age attained by limpets varies greatly according to the species involved, the food potential of the particular habitat, and the zone in which the species occurs. Fretter and Graham (1962, p. 501), quoting Russell (1909), recorded that *Patella vulgata* from certain established populations in Scotland attained a length of about 29 mm. in the first year, during which time they

reached sexual maturity. The estimated sizes reached for each of the four succeeding years were respectively 38, 44, 48 and 53 mm. On the other hand, the same species under more favourable conditions at Plymouth reached a length of 53 mm. by the end of the second year. The estimated life span for *vulgata* is about 15 years.

Very large and massive species, such as *mexicana* and *kermdacensis*, probably live for a much longer time, but size is governed also by the availability of a suitable rock substrate, not unduly encroached upon by barnacles, corals, or other encrusting marine growths. In the tropical Indo-Pacific it is unusual to find large-sized limpets associated with coral reefs, unless there are intrusions of basaltic lava. In general large-sized limpets are more frequent in cool-temperate waters than they are in the tropics.

Limpets that live in the upper tidal zone are usually taller than individuals inhabiting the lower tidal zone. Fretter and Graham (1962, p. 501), quoting Orton (1932), correlated these differences with the degree of exposure to desiccation. Limpets living near low water mark remain exposed for only a short period by the tide, but high-water limpets are uncovered for the greater part of the day, and this results in a general drying out of the habitat.

To prevent desiccation the limpet must hold firmly to the rock for the whole period that it is out of water, and it is suggested that this constant application of force by the attachment muscles tends to pull in the mantle skirt, which is responsible for new growth around the shell margin. This produces a taller and narrower shell than that produced by an animal living lower down in the tidal zone.

Limpets from very exposed situations often appear to be very different from examples living in more sheltered situations. In the exposed examples, the shell becomes very flat in order to withstand wave stress. As a result of this lowered profile, the apex is located nearer to the anterior end.

The colour patterns exhibited by juvenile limpets tend to be less variable than those in more mature examples of the same species, and often provide more satisfactory diagnostic criteria. This is especially evident in *Cellana strigilis* populations from the southern islands of New Zealand (Powell, 1955, pp. 65-67).

Surface erosion of the shell also greatly alters the colour pattern. Thomson (1919, pp. 264-267) described how erosion in *Cellana radians* often eliminates the transverse "earlii" pattern, but

the pigmentation of the radial ribs survives due to deeper impregnation of the shell substance. With the shrinkage of the animal in senile examples, a thick, unicoloured callus is built up on the inside of the shell, blotting out any maculations that may have survived external erosion.

The Patellidae are the most successful and the most advanced family of the Patellacea. The change from a simple leaf-shaped ctenidium in the Acmaeidae, to a gill cordon in the Patellidae results in more efficient aeration. Although *Scurria* and *Lottia* have developed a gill cordon they still retain the acmaeid ctenidium. In the Patellidae the ctenidium has entirely disappeared, leaving the gill cordon as the sole means of respiration.

Patellid limpets have become so successful in their chosen littoral environment that in some locations, South Africa in particular, certain species have become the dominant organisms of several animal communities. In the "Cochlea zone" of South Africa the species *Patella cochlea* is so abundant that almost all other forms of animal life are crowded out. A density of 1,300 individuals of this limpet to the square yard has been recorded, in so dense a concentration that as many as 40 small individuals were found crowded on top of a single large shell.

The radula

The radula in the Patellidae is long and narrow, especially in *Cellana*, in which it sometimes has a length of as much as four times that of the shell. In situ it is concentrated in loose coils on the left hand side when viewed from above. On the other hand, *Patella* has a much shorter radula that folds back upon itself at the nascent end.

The *Patella* radula consists of a strong or weak or rarely absent median central, flanked by a pair of centrals on either side, followed by a large pluricuspid lateral, and finally, three weak, slender, functionless marginals. The latter may be fused into a single plate. Well-developed cusps, capped with a dark stain containing magnetite, are present on the multiple centrals and the pluricuspid laterals, but cusps on the remaining teeth are small to vestigial, and colourless.

In *Cellana* and *Nacella* the radula differs from that of *Patella*, in that the functional teeth are a pair of long, large, centrals, closely-spaced, on either side of a vestigial plate, which also may be absent, alternating with a wider-spaced pair of similar, well-developed laterals; the functionless marginals are as in *Patella*.

In *Patella* the multiple centrals and the large pluricuspid lateral have relatively short recurved cusps, but in *Cellana* and *Nacella*, the alternating pairs of centrals and laterals are very long and project arcuately upward, almost at right angles to the base. These long, strongly upcurved teeth present difficulty in slide preparation, for they are easily pressed at varying angles in mounting, and thus may assume very different shapes. A satisfactory solution to this problem is in the use of cavity slides, that bridge the radula across, so that the teeth assume their normal upright position over the cavity, but are pressed sideways, beyond the limits of the cavity, thus giving details of denticles or indentations along the sides of the teeth.

Many writers have endeavoured to use the length of the radula in relation to the length of the shell for separating three assumed closely allied English *Patella*. The range of the means arrived at by Fretter and Graham (1962, p. 495) is tabulated below.



Plate 61. Fig. 1. *Patella vulgata* Linnaeus; England. Radula. Fig. 2. *Patella caerulea* Linnaeus; Trieste. Radula, from Thiele, in Troschel and Thiele, 1891, pl. 28, fig. 18.

vulgata intermedia aspera

Length of radula	1.51-1.75	1.60-2.10	1.05-1.15
Length of shell			

Unfortunately, in that work, there is no precise indication of the actual identity of the species termed *Patella intermedia*, there being four different usages of that combination by four different authors.

Brian and Owen (1952, pp. 241-249) provided a useful table, giving the valid name equivalents for the nomenclature used in papers on European Patellidae, published up until 1948 (see under heading of *Patella intermedia* Auct.). Following is the summary of Brian and Owen's conclusions.

"*Patella vulgata* L. were collected from high- and low-water levels on five different beaches and the lengths of the shells and radula measured. In all five localities the mean shell length was less and the mean radula length greater at the higher level, but the difference was not consistently significant."

"The complexity arose from the mergence of two conflicting tendencies: one, intralevel, a positive regression of shell-length and radula. While the former is no doubt a growth phenomenon, the latter is probably an environmental effect—at higher level exposure to desiccation and consequently, prolonged adherence to the substrate, caused a smaller shell base; reduced feeding time caused a longer radula. These factors may have resulted in confusion when comparing the values of the radula fractions of species of *Patella*."

Lowenstam (1962) has shown that the radular teeth in the limpets, *Acmaea*, *Lottia* and *Patella*, are capped with goethite, a dark opaque mineral of high iron content. This gives the dark-stained primary cusps of the patellacea a hardness of almost 5 on the Moho hardness scale, whereas the radular hardness in the Littorinidae, the Fissurellidae and certain trochoids is only between 2 and 3.

This hardness factor in the radula enables limpets to erode limestone and other rocks of comparable hardness, as well as the external surface of other shells. Limpets frequently excavate deep depressions in the rock to form a base of attachment, and are known to return to their own particular site after a nightly foraging excursion.

Lowenstam (1962a) also suggested that since, in the case of chitons, the dark stained denticle caps show the presence of magnetite, then it is possible that these magnetised teeth may serve as a guidance system for the so-called homing instinct of both chitons and limpets.

Geographical Distribution of the Patellacea

The family Patellidae has achieved a very wide distribution, extending from near the Arctic Circle to the Antarctic Circle, the western Atlantic, Mediterranean, West and South Africa, the Indo-Pacific to as far north as northern Japan, eastward to the Hawaiian Chain and the Island of Juan Fernandez, and southward to Australia, New Zealand, the subantarctic of the southern end of South America, the islands of the Southern Ocean, and even a few locations adjacent to the Antarctic Continent.

Strangely, there are no patellids on either the east or the west coasts of North America, the Caribbean and most of South America. The only exceptions are the giant *Patella (Ancistromes)* *mexicana* from tropical Central America, obviously derived from the Indo-Pacific when the former Tethys Sea was an open waterway around the perimeter of the globe, and the cold water *Nacella-Patinigera* complex that is strongly represented in southern Patagonia and Chile, and from there spread eastward to the islands of the Southern Ocean.

The Recent distributional patterns for each of the three families of the Patellacea are outlined below (see plate 62).

Acmaeidae: The typical genus, *Acmaea*, is of worldwide distribution, but has its greatest development in western North America, where it takes the place of the Patellidae, members of which are absent from that area. Two other genera of the Acmaeidae, *Scurria* and *Lottia*, are apparent forerunners of the Patellidae, since they have developed pallial gills, additional to the single gill-plume of typical *Acmaea*. Their present range is along the west coast of both North and South America.

Patellidae: Typical *Patella* is well-represented along the western coast of Europe, from the Lofoten Islands to Great Britain, down to Spain, the Mediterranean, the West African mainland and off-shore islands, then southward to South Africa, where typical *Patella* becomes more or less merged into a composite local fauna of cold and warm-water subgenera. From there the genus continues, in subgeneric form, across to the warmer water island groups of the Indo-Pacific, extending northward to Japan, eastward to the west coast of tropical Central America, and southward to the Kermadec Islands and the temperate waters of southern Australia and Tasmania.

The genus *Cellana* is confined for the most part to the warm and cool temperate waters of the

Indo-Pacific, but in the New Zealand area it actually extends southward into subantarctic waters. The farthest westward reached by *Cellana* is the coast of Natal, the farthest eastward the island of Juan Fernandez, off the coast of Chile, and the farthest northward, Japan.

A third major genus in this family is *Nacella*, containing the important subgenus *Patinigera*. These are truly cold-water limpets, the greater part of their range being subantarctic, but extending to the Antarctic by way of the Scotia Arc, and also ranging northward up the Chilean coast to at least Valparaíso, assisted in this by the upwelling of cold water along that coast. The present concentration of the genus is in the Magellanic area, and from there it spreads eastward, assisted in this by the prevailing West Wind Drift. Many of the species live upon the large kelps which provide an effective means of chance dispersal when quantities of the weed are wrenched free and drift before wind and current. The farthest eastward that this genus has established itself is Kerguelen Island, and for the subgenus Campbell Island in the New Zealand southern islands.

The genus *Nacella* and its subgenus *Patinigera* have a distinctive epipodial fringe, not found so far in any other genus of the Patellacea. The European Tertiary fossils attributed to *Nacella* probably belong to other genera.

Lepetidae: This family consists of rather small featureless white limpets, mainly from the deeper waters of the Arctic Ocean, the north Atlantic, the north Pacific, Mediterranean, Patagonia and Antarctica. They are rather specialised, but not necessarily highly advanced. There are no gills, and respiration takes place through a cilia-lined pallial groove. The presence of a large, broad-based central tooth, with a conspicuous, broadly-triangular, dentate cusp, no laterals, but a pair of functional marginals, are radular characters not found in the other two living families of the Patellacea.

Fossil Occurrences of the Patellidae

Although a considerable number of fossil so-called *Patella* species are encountered in literature, especially those from European Tertiary localities, few of them can be assigned with certainty to that genus. The problem faced by workers with Recent species of the Patellacea, that of distinguishing between the Acmaeidae and the Patellidae when the animal is unknown, is even more a matter of conjecture when fossil species are under consideration, especially with those from the older formations, that have shell features unlike those of living species.

The earliest species of the Patellidae that can be generically identified with some degree of con-

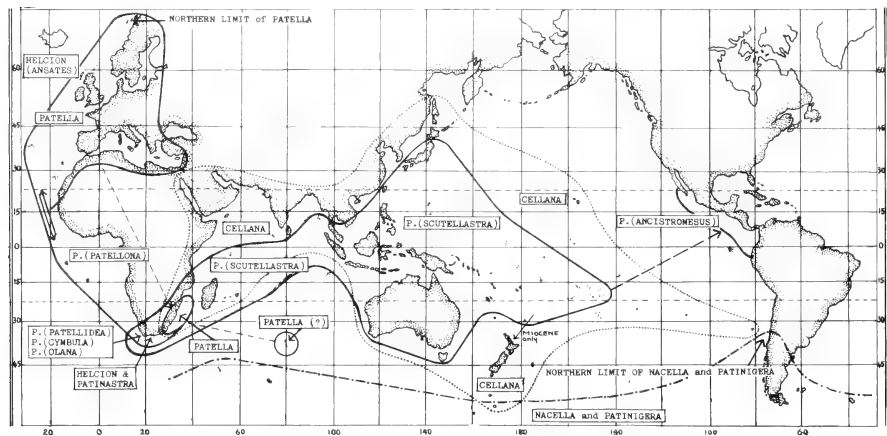
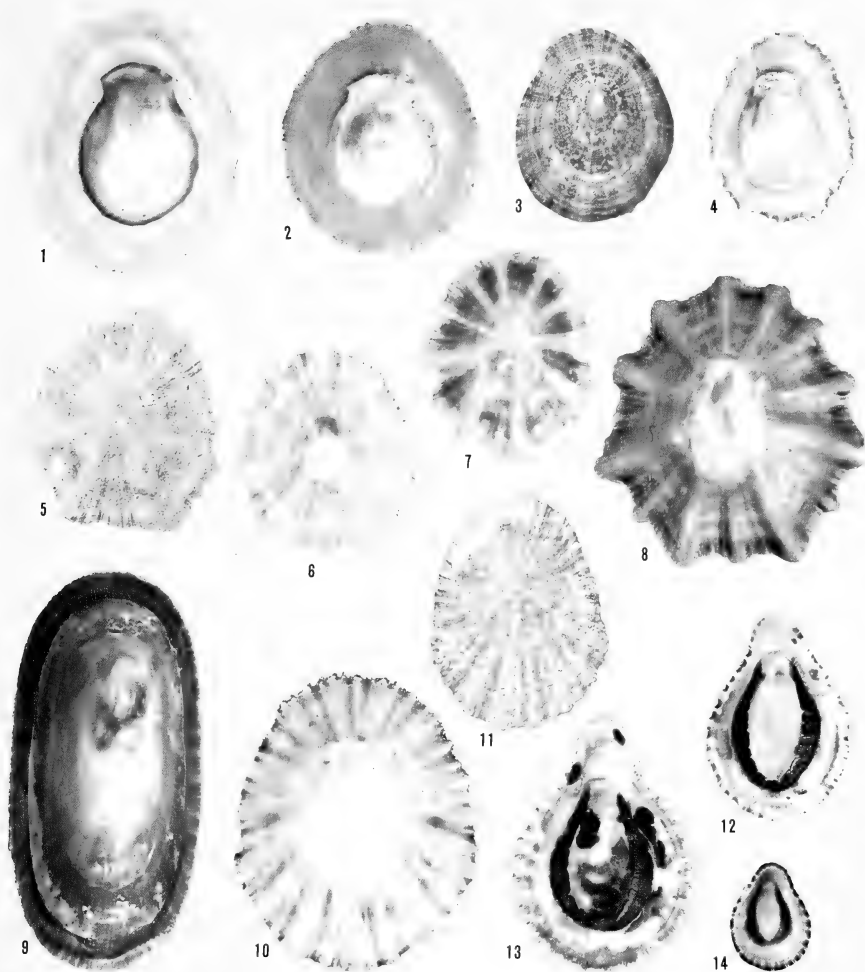


Plate 62. Geographical distribution of the Patellidae. Note the almost entire absence of the family from North America, and most of South America, with the exception of one species, *Ancistromes mexicana*, which occurs along the west coast

of Central America, and *Nacella*, with its subgenus *Patinigera*, in the southern part of South America, from where it has drifted eastward over much of the Subantarctic and in some areas of the Antarctic.

Plate 63. European and South Africa *Patella*

Figs. 1-3. *Patella vulgata* Linnaeus, 1758. Figs. 1, 2. Caldy Island, South Wales. Fig. 3. Ilfracombe, England.

Fig. 4. *Patella aspera* Röding, 1798. Caldy Island, South Wales.

Figs. 5-7. *Patella caerulea* Linnaeus, 1758. Isle of Capri, Italy.

Fig. 8. *Patella caerulea* Linnaeus, 1758 (forma *crenata* Gmelin, 1791). Madeira.

Fig. 9. *Patella (Cymbula) compressa* Linnaeus, 1758. Kommetje, Cape Peninsula, South Africa. Lives on large kelp; always sideways compressed.

Figs. 10, 11. *Patella (Cymbula) miniata* Born, 1778. Fig. 10. False Bay, South Africa. Fig. 11. Port Elizabeth, South Africa; beach shells bleach to bright pink.

Figs. 12-14. *Patella (Olana) cochlear* Born, 1778. Sea Point, South Africa. Anterior end always constricted like a spout.

fidence are *Cellana carpentariana* Skwarko, 1966, from the late Neocomian lower Cretaceous of Northern Territory, Australia, and *Patella (Scutellastra) cooperi* (Powell, 1938) from the Otaian Stage, lower Miocene of Motuihi Island, Auckland, New Zealand.

The above two records show at least that the separation of *Patella* and *Cellana* is of long standing, and coupled with the radular divergence, justifies Thiele's division of the family into two subfamilies, the Patellinae Rafinesque, 1815, and the Nacellinae Thiele, 1929.

Doubtful species of Patellidae

Patella ? *amurita* Wilkens, 1922

Range—New Zealand, Amuri Bluff, upper Cretaceous.

Remarks—This species is based upon a very damaged and incomplete shell only 5 mm. in length. The whole of the apical area is missing and only a ring of shelly material remains. Even Wilkens expressed doubt as to whether his generic determination was correct.

Synonymy—

1922 *Patella* ? *amurita* Wilkens, N. Z. Geol. Surv. Pal. Bull. no. 9, p. 5, pl. 1, fig. 8.

Patella guineensis Dunker, 1853

Remarks—The present writer has insufficient West African material to evaluate Dunker's species, the name of which is preoccupied by *Patella guineensis* Gmelin, 1791.

Synonymy—

1853 *Patella guineensis* Dunker, Ind. Moll. Guin. Infer., p. 40, pl. 7, figs. 1-3; 19-21. Loanda, Guinea, West Africa [Angola].

Cellana jutsoni Chapman and Crespin, 1934

Remarks—This species, from the lower Miocene Plantagenet Beds of Albany, Western Australia, is very doubtfully patellid. The presence of an "obscure ridge, extending from the apex to the posterior margin" suggests the fissurellid genus *Tugali* or something akin to it.

Synonymy—

1934 "*Cellana*" *jutsoni* Chapman & Crespin, Journ. Roy. Soc. West. Aust., vol. 20, p. 122, pl. 11, fig. 28.

Patella aspera Röding, 1798

(Pl. 63, fig. 4; pl. 68, figs. 3, 4)

Range—British Isles and Atlantic coast of France.

Remarks—This "species" is not always readily distinguished from *vulgata*. Typically it is more elongated than *vulgata*, depressed, with the apex nearer to the anterior end, and the primary ribs are stronger and sharper, resulting in a more definitely corrugated margin. Other differences are that the interior is porcellaneous whitish, with the head scar pale orange, radial colour lines are sub-obsolete to obsolete, and the colour of the foot of the animal is cream to orange, as opposed to grey-green in *vulgata*.

Measurements (mm.)—

length	width	height	
53.0	42.0	21.0	Caldy Id., South Wales
47.0	35.5	20.0	Caldy Id., South Wales

Synonymy—

1798 *Patella aspera* Röding, Mus. Bolten., vol. 2, p. 10 (refers to Favanne, pl. 2, f. G).

1819 *Patella aspera* Lamarck, Anim. sans Vert., vol. 6, p. 327 (refers to Favanne, pl. 2, f. G).

1844 *Patella athletica* Bean, in Thorpe, Brit. Mar. Conch., p. 264, fig. 101).

1968 *Patella aspera* Lam., McMillan, Brit. Shells, Warne & Co. Ltd., London. New York, p. 25, pl. 1, figs. 1, 3, 4.

Patella depressa Pennant, 1777

Range—South coast of England, Channel Islands and Atlantic coast of France.

Remarks—This is the small, very depressed, *Siphonaria*-like species, or form of *vulgata*, of which *Patella vulgata* var. *intermedia* Jeffreys, 1865 is a synonym. Jeffreys described his variety *intermedia* as "Shell rather smaller, flatter, and oval, with finer ribs, and an orange crown; inside golden-yellow or tinged with flesh colour (occasionally cream colour) in the centre, and beautifully rayed toward the margin." Forbes also remarked that the animal is black or dark-coloured.

Despite the detailed studies of both Fischer-Piette and R. G. Evans, the taxonomic status of both *aspera* and *depressa* in relation to *vulgata* is still uncertain. Evans endeavoured to separate the three as full species, upon minute differences in the pluricuspid radula teeth, coupled with the varying lengths of the radula for each. In dealing with populations from the south of England Evans admitted, that at the Isle of Wight, intermediate forms were common but then remarked that to the westward along the south coast three species form discontinuous entities.

Synonymy—

- 1777 *Patella depressa* Pennant, Brit. Zool., vol. 4, p. 124, pl. 89, fig. 146.
 1865 *Patella, vulgata* var. *intermedia* Jeffreys, Brit. Conch. vol. 3, p. 237.
 1923 *Patella depressa* Pennant, Tomlin, Journ. Conch., vol. 17, p. 34.
 1935 *Patella* spp. Fischer-Piette, Systematique et biogeographie-Les Patelles d'Europe et d'Afrique du Nord, Journ. Conchyl., vol. 79, pp. 5-66.
 1952 *Patella depressa* Pennant, Evans, Proc. Zool. Soc., Lond., pp. 357-376.

Patella electrina Reeve, 1854

Remarks—This shell, described as coming from Australia, is unlike any species known from that area. Examination of the type specimen in the British Museum (Natural History) revealed a *Patella* of the *caerulea* series, very like the Canary Islands *Patella lowei* d'Orbigny, so far as one can judge from a single example.

Synonymy—

- 1854 *Patella electrina* Reeve, Conch. Iconica, pl. 22, fig. 55a, b.

Patella intermedia

Many writers have attempted to give taxonomic status to the forms of both *vulgata* and *caerulea* by providing detailed studies of the radulae, particularly its length in relation to that of the shell (see also, under the heading "Radula," in the introduction), in small differences in the pluricuspid laterals, and also in the colour of the foot of the animal.

Unfortunately with many of these papers it is difficult to correlate the results with the species or forms investigated, due to a common fault of many anatomists of placing little or no importance upon the characters of the shell, and seldom illustrating the relevant shells.

Another source of confusion is in the nomenclature employed, specific names being frequently cited without their respective authority and date. A name that is quoted frequently, and around which much useful data is associated is "*intermedia*," but which patellid of that name is intended?—that of Knapp, 1857, Jeffreys, 1865, or Bucquoy, Dautzenberg and Dollfus, 1882?

Brian and Owen (1952) endeavoured to rectify this confusion by concluding that *P. intermedia* Jeffreys, 1865, as used by Fischer-Piette (1935, 1938 and 1948), Eslick (1940) and Orton (1946) was *Patella depressa* Pennant, 1777. They also concluded that *P. athletica* Bean, 1844, as used

in the Plymouth Marine Fauna (1931) and by Winckworth (1932) and Evans (1947) and *P. depressa*, as used by Fischer-Piette (1935), Eslick (1940) and Orton (1946) were all *Patella aspera* Lamarck (now *aspera* Röding, 1798).

The earliest use of the name *intermedia*, in association with *Patella*, is that of Knapp, in Murray, 1857, proposed for a Channel Islands shell, that appears to be a form of *Patella vulgata* Linnaeus, 1758.

Patella lineata Lamarck, 1819

Remarks—This shell, from unknown locality, was referred to *Helcioniscus* (now *Cellana*) by Pilsbry, but Delessert's figures suggest a species of the Acmaeidae. Pilsbry's translation of Lamarck's description follows:

Description—"Shell oval, convex, buff-brown, painted with 10-12 yellow lines; excessively numerous longitudinal close striae; vertex acute, buff. Length exceeding one inch."—27 mm. (Mermoud).

Synonymy—

- 1819 *Patella lineata* Lamarck, Anim. sans vert., vol. 6 (1), p. 331; *Patella lineata* Delessert, Rec. de Coq., pl. 23, fig. 6.
 1891 *Helcioniscus lineatus* Lamarck, Pilsbry, Man. of Conch., vol. 13, p. 153, pl. 73, figs. 85-87.
 1950 *Patella lineata* Lamarck, Mermoud, Revue Suisse de Zool., vol. 57, no. 34, p. 694 (remarks on the type).

? Patella nelsonensis Trechmann, 1918

Range—Nelson, New Zealand, lower conglomerates, lower slopes of range, upper end of Eighty-eight Valley, Kaihikuan Stage, middle Triassic.

Remarks—The holotype and two paratypes are in the New Zealand Geological Survey, Wellington, but the preservation is not good enough to show muscle scars, hence it cannot be determined, on the present material, whether the apex is directed anteriorly or posteriorly. The species remains a doubtful member of the Patellacea.

Synonymy—

- 1918 *Patella* (?) *nelsonensis* Trechmann, Quart. J. Geol. Soc., vol. 73, pt. 3, p. 185, pl. 18, figs. 8 a, b.
 1953 *Patella nelsonensis* Trechmann, Marwick, N. Z. Geol. Surv. Pal. Bull. no. 21, p. 74, pl. 7, fig. 3.

Patella reussi K. Martin, 1879

Remarks—This species from the Miocene of Java could be fissurellid. The figure shows a shell embedded in matrix, and in consequence the interior

of the shell, with its muscle impressions, is unknown.

Synonymy—

1879 *Patella reussi* K. Martin, Die Tert. auf Java, Leiden, p. 87, pl. 12, fig. 9.

Patella spectabilis Dunker, 1853

Remarks—The description and figures of Dunker's species suggest a form of *Patella lowei* d'Orbigny, 1839. However, Dunker's name is preoccupied by *Patella spectabilis* Gmelin, 1791.

Synonymy—

1853 *Patella spectabilis* Dunker, Ind. Moll. Guin. Infer., p. 39, pl. 6, figs. 7-9. Loanda, Guinea, West Africa [Angola].

Species no longer included in the Patellidae

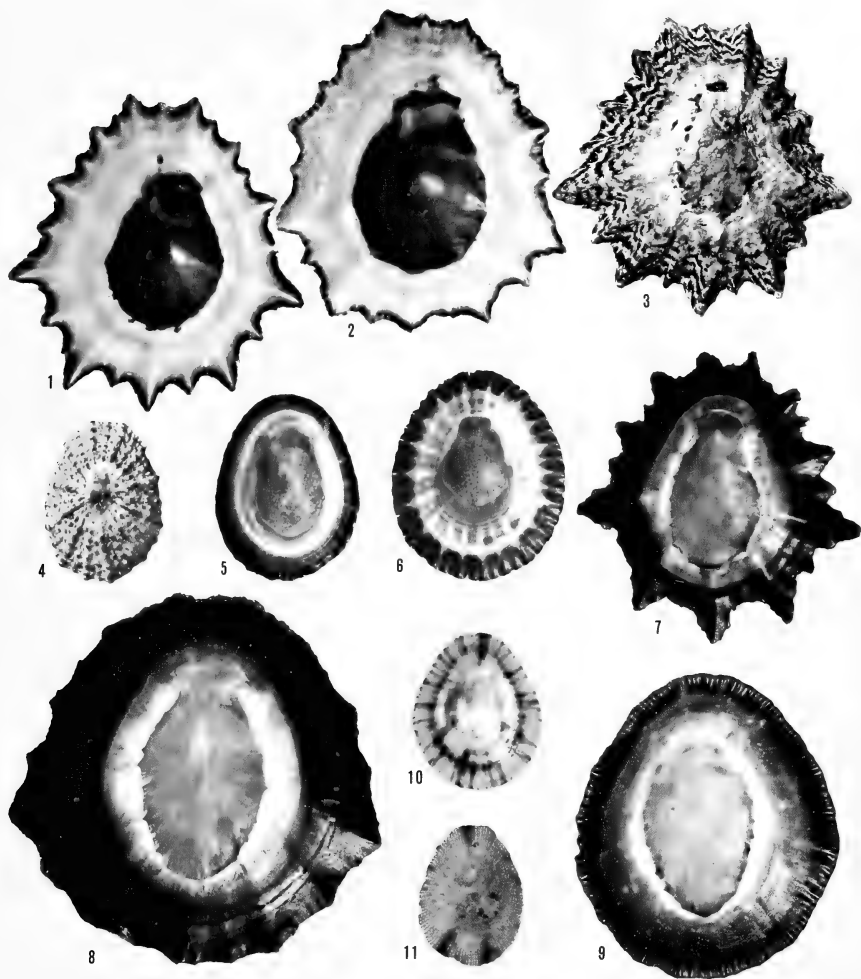
The following species, originally referred to the Patellidae, are now known to belong to other families. This list includes only species that the writer has been able to evaluate, either personally, or upon the authority of subsequent revisers. There remains a considerable number of patellid names yet to investigate, but since many of these have been inadequately described, seldom figured, and often without locality data, it is probable that most, eventually, will have to be considered indeterminate.

Species prefixed by an asterisk (*) are the subject of a note at the conclusion of this section.

The writer has compiled a manuscript list of over 1,250 patellid names encountered in the preparation of the present work, but it is withheld from publication at this stage, since it cannot be considered reasonably complete, without a more thorough appraisal of European species, the fossil ones in particular. A dagger (†) precedes fossil species in this list.

achates Reeve, 1855, <i>Patella</i>	Acmaeidae
acimaces Lea, 1846, <i>Patella</i>	? Pholadidae
aculeata Gmelin, 1791, <i>Patella</i>	Calyptraeidae
adunca Perry, 1811, <i>Patella</i>	Fissurellidae
aenigmatia Mahille, 1895, <i>Patella</i>	Acmaeidae
aeruginosa Middendorff, 1847, <i>Patella</i> (Acmaea) ..	Acmaeidae
afra Gmelin, 1791, <i>Patella</i>	Trimusculidae
albescens Anton, 1839, <i>Patella</i>	Acmaeidae
albicosta C. B. Adams, 1855, <i>Patella</i>	Acmaeidae
albicostata Reeve, 1855, <i>Patella</i>	Acmaeidae
alticostata Angas, 1865, <i>Patella</i>	Acmaeidae
alveus Conrad, 1831, <i>Patella</i>	Acmaeidae
ambigua Wood, 1818, <i>Patella</i>	Fissurellidae
amoenia Say, 1822, <i>Patella</i>	Acmaeidae
ancyloides E. Forbes, 1840, <i>Patella</i>	Lepetidae
ancyloides Middendorff, 1847, <i>Patella</i> (Acmaea) ..	Acmaeidae
angulata Wood, 1828, <i>Patella</i>	Calyptraeidae
angusta Gmelin, 1791, <i>Patella</i>	Fissurellidae

antillarum Philippi, 1849, <i>Patella</i> (Acmaea)	Acmaeidae
antiquata Linnaeus, 1767, <i>Patella</i>	Hipponicidae
apertura Montagu, 1803, <i>Patella</i>	Fissurellidae
araneosa Gould, 1848, <i>Patella</i>	Acmaeidae
araneosa Reeve, 1855, <i>Patella</i>	Acmaeidae
aracana d'Orbigny, 1841, <i>Patella</i>	Acmaeidae
asmi Middendorff, 1847, <i>Patella</i>	Acmaeidae
atricapilla Dillwyn, 1817, <i>Patella</i>	Fissurellidae
auricula Gmelin, 1791, <i>Patella</i>	Calyptraeidae
auricula W. Wood, 1828, <i>Patella</i>	Stomatellidae
australis Lamarck, 1819, <i>Patella</i>	Hipponicidae
avellana Gmelin, 1791, <i>Patella</i>	Fissurellidae
axiaerata Verco, 1912, <i>Patella</i>	Acmaeidae
balanoides Reeve, 1855, <i>Patella</i>	Acmaeidae
barbadensis Gmelin, 1791, <i>Patella</i>	Fissurellidae
biradiata Reeve, 1855, <i>Patella</i>	Acmaeidae
borneensis Reeve, 1855, <i>Patella</i>	Acmaeidae
borniana Helbing, 1779, <i>Patella</i>	Acmaeidae
caeca Müller, 1776, <i>Patella</i>	Lepetidae
calamus Crosse & Fischer, 1864, <i>Patella</i>	Acmaeidae
callosa Hombron & Jacquinot, 1841, <i>Patella</i>	Acmaeidae
campaniformis Blainville, 1825, <i>Patella</i>	? Siphonariidae
campbelli Filhol, 1880, <i>Patella</i>	Acmaeidae
cancellata Gmelin, 1791, <i>Patella</i>	Acmaeidae
candida Couthouy, 1838, <i>Patella</i>	Lepetidae
cantharus Reeve, 1855, <i>Patella</i>	Acmaeidae
caissida Dillwyn, 1817, <i>Patella</i>	Hipponicidae
casta Carpenter, 1866, <i>Nacella</i>	Acmaeidae
ceciliana d'Orbigny, 1841, <i>Patella</i>	Acmaeidae
cerea Möller, 1842, <i>Patella</i>	Lepetidae
chilensis Blainville, 1825, <i>Patella</i>	? Siphonariidae
chinensis Linnaeus, 1758, <i>Patella</i>	Calyptraeidae
cineliata Reeve, 1855, <i>Patella</i>	Acmaeidae
cinis Reeve, 1854, <i>Patella</i>	Acmaeidae
cinnamomea Gould, 1846, <i>Patella</i>	Phenacolepadidae
clealandi J. Sowerby, 1822, <i>Patella</i>	Acmaeidae
clypeus T. Brown, 1827, <i>Patella</i>	Acmaeidae
cochleata Dillwyn, 1817,	Capulidae
coffea Reeve, 1855, <i>Patella</i>	Acmaeidae
compressiuscula Karsten, 1849, <i>Patella</i>	Acmaeidae
concentrica Middendorff, 1851, <i>Patella</i>	Lepetidae
conceptionis Lesson, 1831, <i>Patella</i>	Acmaeidae
concinna Lischke, 1870, <i>Patella</i>	Acmaeidae
conica Defrance, 1825, <i>Patella</i>	Acmaeidae
conica Gould, 1846, <i>Patella</i>	Acmaeidae
conulus Dunker, 1882, <i>Patella</i>	Acmaeidae
corrugata Reeve, 1854, <i>Patella</i>	Acmaeidae
craniolaris Röding, 1798, <i>Patella</i>	Fissurellidae
crebrestriata Verco, 1904, <i>Nacella</i>	Acmaeidae
crepidula Linnaeus, 1764, <i>Patella</i>	Calyptraeidae
cruciata Linnaeus, 1758, <i>Patella</i>	Acmaeidae
crystallina W. Wood, 1828, <i>Patella</i>	Fissurellidae
cubensis Reeve, 1855, <i>Patella</i>	Acmaeidae
cumingii Reeve, 1854, <i>Patella</i>	Acmaeidae
diaphana Reeve, 1854, <i>Patella</i>	Acmaeidae
dichotoma Anton, 1839, <i>Patella</i>	Acmaeidae
digitale Röding, 1798, <i>Patella</i>	Acmaeidae
discors Philippi, 1849, <i>Patella</i> (Acmaea)	Acmaeidae
elegans Philippi, 1849, <i>Patella</i>	Acmaeidae
emarginuloides Philippi, 1865, <i>Patella</i>	Lepetidae
equestris Linnaeus, 1758, <i>Patella</i>	Calyptraeidae
exilis Philippi, 1849, <i>Patella</i>	Acmaeidae
fenestrata Reeve, 1855, <i>Patella</i>	Acmaeidae
fimbriata Gould, 1846, <i>Patella</i>	Acmaeidae
fissura Linnaeus, 1758, <i>Patella</i>	Fissurellidae
fissurata Dillwyn, 1817, <i>Patella</i>	Fissurellidae
fissurella O. F. Müller, 1776, <i>Patella</i>	Fissurellidae
floccata Reeve, 1855, <i>Patella</i>	Acmaeidae
fluxuitalis Gmelin, 1791, <i>Patella</i>	Ancylidae
forbesii J. Smith, 1839, <i>Patella</i>	Lepetidae
formicata Linnaeus, 1758, <i>Patella</i>	Calyptraeidae
fulva O. F. Müller, 1776, <i>Patella</i>	Lepetidae
fungoides Röding, 1798, <i>Patella</i>	Acmaeidae

Plate 64. South African *Patella*

Figs. 1-3. *Patella (Patellona) granatina* Linnaeus, 1758. Sea Point, South Africa.

Figs. 4-6. *Patella (Patellidea) granularis* Linnaeus, 1758. Sea Point, South Africa.

Figs. 7-9. *Patella (Patellona) oculus* Born, 1778. Buffel's Bay, Cape Peninsula, South Africa.

Figs. 10-11. *Patella concolor* Krauss, 1848. Near Durban, Natal.

galathea Lamarck, 1819, Patella	Phenacolepadidae	onychites Menke, 1843, Patella	Acmaeidae
goeensis Gmelin, 1791, Patella	Calyptraeidae	topea Reeve, 1854, Patella	Acmaeidae
gracila Linnaeus, 1758, Patella	Fissurellidae	oregona Nuttall, 1839, Patella	Acmaeidae
grammia Philippi, 1847, Patella	Acmaeidae	pallensens Philippi, 1849, Patella (Acmaea)	Acmaeidae
granostriata Schrenck, 1867, Patella	Acmaeidae	palidula Gould, 1859, Patella	Acmaeidae
granulata Philippi, 1848, Patella	Acmaeidae	papillaris Röding, 1798, Patella	Acmaeidae
grisea Gmelin, 1791, Patella	Siphonariidae	parastica d'Orbigny, 1841, Patella	Acmaeidae
grisea Röding, 1798, Patella	Fissurellidae	parva da Costa, 1778, Patella	Acmaeidae
haliotidea Röding, 1798, Patella	Calyptraeidae	patina Eschscholtz, 1847, Patella (Acmaea)	Acmaeidae
hepatica Pritchard & Gatliff, 1903, Patella	Acmaeidae	pectinata Linnaeus, 1758, Patella	Siphonariidae
heptagona Blainville, 1825, Patella	Acmaeidae	pediculus Philippi, 1846, Patella	Acmaeidae
heroldi Dunker, 1882, Patella	Acmaeidae	peltoides Carpenter, 1864, Nacella	Siphonariidae
hiantula W. Wood, 1828, Patella	Fissurellidae	penicillata Reeve, 1855, Patella	Acmaeidae
*hochstetteri K. Martin, 1879, Patella	Fissurellidae	perforata Gmelin, 1791, Patella	Fissurellidae
incisa Dillwyn, 1817, Patella	Fissurellidae	persona Eschscholtz, 1847, Patella (Acmaea)	Acmaeidae
inconspicua Gray, 1843, Patella	Acmaeidae	personata T. Martyn, 1788, Patella (non binom.)	Fissurellidae
indica W. Wood, 1828, Patella	Umbraculidae	perversa Gmelin, 1791, Patella	Umbraculidae
inradiata Reeve, 1855, Patella	? Acmaeidae	personoides Middendorff, 1849, Patella (Acmaea)	Acmaeidae
inessa Hinds, 1842, Patella	Acmaeidae	peziza W. Wood, 1828, Patella	Calyptraeidae
insignis Menke, 1843, Patella	Acmaeidae	phyrozonias Gmelin, 1791, Patella	Fissurellidae
instabilis Gould, 1846, Patella	Acmaeidae	picta Gmelin, 1791, Patella	Fissurellidae
intertexta Röding, 1798, Patella	Acmaeidae	pilcolus Dillwyn, 1817, Patella	Fissurellidae
jacksoniensis Reeve, 1855, Patella	Acmaeidae	pilcolus Middendorff, 1849, Patella (Acmaea)	Acmaeidae
jamaicensis Gmelin, 1791, Patella p. 3715	Acmaeidae	plana Philippi, 1849, Patella	Acmaeidae
jamaicensis Gmelin, 1791, Patella, p. 3730	Fissurellidae	plana Reeve, 1855, Patella	Acmaeidae
javonica Lamarck, 1819, Patella	Siphonariidae	poculum W. Wood, 1828, Patella	Calyptraeidae
kochi Philippi, 1849, Patella	Acmaeidae	pretrei d'Orbigny, 1841, Patella	Acmaeidae
laciniata Reeve, 1855, Patella	Acmaeidae	profunda Deshayes, 1863, Patella	Acmaeidae
laciniosa Linnaeus, 1758, Patella	Siphonariidae	punctatissima Philippi, 1849, Patella	Acmaeidae
lacunosa Reeve, 1855, Patella	Acmaeidae	punctulata Gmelin, 1791, Patella	Acmaeidae
lacustris Linnaeus, 1758, Patella	Ancylidae	puncturata Lamarck, 1819, Patella	Acmaeidae
lamanonii Schrenck, 1867, Patella	Acmaeidae	pustula Gmelin, 1791, Patella	Fissurellidae
lanx Reeve, 1855, Patella	Acmaeidae	pustulata Helbling, 1779, Patella	Acmaeidae
laqueare W. Wood, 1828, Patella	? Acmaeidae	pygmaea Dunker, 1882, Patella	Acmaeidae
latistrigata Angus, 1865, Patella	Acmaeidae	rosea Gmelin, 1791, Patella	Fissurellidae
lenticinosa Reeve, 1855, Patella	Acmaeidae	rosea Dall, 1872, Nacella ?	Acmaeidae
lepas Gmelin, 1791, Patella	Muricidae (Thaidinae)	roseoradiata Verco, 1912, Nacella crebrestriata	Acmaeidae
leucophaea Philippi, 1849, Patella	Acmaeidae	rubra O. Fabricius, 1780, Patella	Acmaeidae
leucopleura Gmelin, 1791, Patella	Acmaeidae	rubra Röding, 1798, Patella	Fissurellidae
leucopleura Reeve, 1855, Patella	Acmaeidae	rudit Röding, 1798, Patella	Fissurellidae
lima Reeve, 1855, Patella	Acmaeidae	rugosa Röding, 1798, Patella	Capulidae
limbata Röding, 1798, Patella	Fissurellidae	saccharina Linnaeus, 1758, Patella	Acmaeidae
lineata Philippi, 1849, Patella	Acmaeidae	scabra Gould, 1846, Patella (Lottia)	Acmaeidae
*luchuana Pilsbry, 1901, Patella	Acmaeidae	scabra Reeve, 1855, Patella	Acmaeidae
luctuosa Hombron & Jacquinot, 1841, Patella	Acmaeidae	scapula Martyn, 1789, Patella (non binom.)	Aplysidae
lutea Linnaeus, 1758, Patella	Stomatellidae	schrenckii Lischke, 1868, Patella	Acmaeidae
macrochisma Lightfoot, 1786, Patella	Fissurellidae	scurra Lesson, 1831, Patella	Acmaeidae
macrochisma Dillwyn, 1817, Patella	Fissurellidae	scutellata W. Wood, 1828, Patella	Calyptraeidae
mamillata (Nuttall) Reeve, 1855, Patella	Acmaeidae	senilis Röding, 1798, Patella	Umbraculidae
mauritiana Pilsbry, 1891, Helcioniscus	Acmaeidae	smensis Gmelin, 1791, Patella	Calyptraeidae
melanoleuca Gmelin, 1791, Patella	Acmaeidae	sinica Gmelin, 1791, Patella	Umbraculidae
melanoleuca Reeve, 1855, Patella	Acmaeidae	sinosa Brocchi, 1814, Patella	Capulidae
merceuxi Deshayes, 1861, Patella	Acmaeidae	solandri Colenso, 1844, Patella	Acmaeidae
minima Gmelin, 1791, Patella	? Acmaeidae	spectrum Reeve, 1855, Patella	Acmaeidae
nitida Röding, 1798, Patella	Fissurellidae	spinosa Gmelin, 1791, Patella	Fissurellidae
mixta Reeve, 1855, Patella	Acmaeidae	squamulata Renier, 1804, Patella	Calyptraeidae
mülleri Dunker, 1875, Patella (Tectura)	Acmaeidae	stella Lesson, 1831, Patella	Acmaeidae
muricata Brocchi, 1814, Patella	Calyptraeidae	stellaris Reeve, 1855, Patella	Acmaeidae
mytiliformis Gmelin, 1791, Patella	Calyptraeidae	stipulata Reeve, 1855, Patella	Acmaeidae
navicula Reeve, 1854, Patella	Acmaeidae	stovae Verco, 1906, Nacella	Acmaeidae
neptuni Dillwyn, 1817, Patella	Calyptraeidae	striata Reeve, 1855, Patella	Acmaeidae
*nigrosulcata Reeve, 1855, Patella	Acmaeidae	sturnus Hombron & Jacquinot, 1841, Patella	Acmaeidae
nimbosa Linnaeus, 1758, Patella	Fissurellidae	subspiralis Carpenter, 1864, Nacella	Siphonariidae
noachina Linnaeus, 1771, Patella	Fissurellidae	sulcata Borson, 1820, Patella	Hipponicidae
nodosa Born, 1778, Patella	Fissurellidae	tectum Dillwyn, 1817, Patella	Calyptraeidae
notata Linnaeus, 1758, Patella	Fissurellidae	tectumchinensis Röding, 1798, Patella	Calyptraeidae
nubecula Linnaeus, 1758, Patella	Fissurellidae	tenera C. B. Adams, 1845, Patella	Acmaeidae
nummularis Röding, 1798, Patella	Fissurellidae	tenuicostata Michelin, 1838, Patella	Acmaeidae
nuballiana Reeve, 1855, Patella	Acmaeidae	tessellata O. F. Müller, 1779, Patella	Acmaeidae
obtusata Koenen, 1892, Patella (Acmaea)	? Cocculinidae	testudinalis O. F. Müller, 1776, Patella	Acmaeidae
obscura Hombron & Jacquinot, 1841, Patella	Acmaeidae	textilis Gould, 1846, Patella (Lottia)	Acmaeidae
occidentalis Reeve, 1855, Patella	Acmaeidae	tranquebarica Gmelin, 1791, Patella	Acmaeidae
octoradiata Gmelin, 1791, Patella	Fissurellidae	triangularis Carpenter, 1866, Nacella paleacea	Acmaeidae

tricarinata Linnaeus, 1767, <i>Patella</i>	Hipponicidae
tricostata Gmelin, 1791, <i>Patella</i>	Hipponicidae
trochiformis Gmelin, 1791, <i>Patella</i>	Calyptraeidae
trochoides Dillwyn, 1817, <i>Patella</i>	Calyptraeidae
tuberculifera Lamarck, 1819, <i>Patella</i>	? Siphonariidae
turcica Röding, 1798, <i>Patella</i>	Calyptraeidae
umbellata Gmelin, 1791, <i>Patella</i>	Umbraculidae
umbellata della Chiaje, 1830, <i>Patella</i>	Umbraculidae
umbonata Reeve, 1855, <i>Patella</i>	Acmaeidae
uncinata Reeve, 1855, <i>Patella</i>	Acmaeidae
undulata Röding, 1798, <i>Patella</i>	Calyptraeidae
ungarica Linnaeus, 1758, <i>Patella</i>	Capulidae
unguis Linnaeus, 1758, <i>Patella</i>	Fissurellidae
unguis J. Sowerby, 1816, <i>Patella</i>	Capulidae
unguisaluae Lesson, 1831, <i>Patella</i>	Acmaeidae
verruculata Reeve, 1855, <i>Patella</i>	Acmaeidae
vespertina Reeve, 1855, <i>Patella</i>	Acmaeidae
victoriae Gatliff & Gabriel, 1922, <i>Patella</i>	Acmaeidae
victoriana Singleton, 1937, <i>Patella</i>	Acmaeidae
virginea O. F. Müller, 1776, <i>Patella</i>	Acmaeidae
viridula Lamarck, 1819, <i>Patella</i>	Acmaeidae
zebrina Lesson, 1831, <i>Patella</i>	Acmaeidae

Notes relevant to the above non-patellid species

Patella hochstetteri K. Martin, 1879

Remarks—This species, from the Miocene of Java, is a *Hemitoma*, family Fissurellidae, in fact its author likened it to *Hemitoma notata* (Linnaeus, 1758).

Synonymy—

- 1879 *Patella hochstetteri* K. Martin, Die tert. auf Java, Leiden, p. 86, pl. 12, fig. 10.

Patella luchuana Pilsbry, 1901

Remarks—Habe determined that the radula and gill structure of this Ryukyu Islands limpet prove it to belong to the Acmaeidae.

Synonymy—

- 1901 *Patella luchuana* Pilsbry, Proc. Acad. Nat. Sci. Phila., vol. 53, p. 202.
1957 *Collisella luchuana* Pilsbry, Habe, Proc. Malac. Soc. Lond., vol. 32, p. 207.

Patella nigrosulcata Reeve, 1855

Remarks—This shell, described from unknown locality, has since been identified as a Western Australian *Patelloida*, family Acmaeidae, and thus has nothing to do with *Patella (Scutellastra) stellaeformis*, where it was assigned as a variety by Pilsbry, 1891. The species is usually found attached to the backs of large *Patella (Scutellastra) laticostata* Blainville.

Synonymy—

- 1855 *Patella nigro-sulcata* Reeve, Conch. Iconica, pl. 30, figs. 84 a, b.
1891 *Patella (Scutellastra) stellaeformis* var. *nigrosulcata* Reeve, Pilsbry, Man. of Conch., vol. 13, p. 100, pl. 66, figs. 66, 67.
1955 *Patelloida nigrosulcata* Reeve, Macpherson, Proc. Royal Society of Victoria, vol. 67 (2), p. 241.

Patella opea Reeve, 1854

Remarks—Dr. Myra Keen has shown that the originally cited locality for this species, "Sandwich Islands" – Hawaii, is incorrect, and that the species is a synonym of the West American *Acmaea fascicularis* Menke, 1851.

Synonymy—

- 1854 *Patella opea* Reeve, Conch. Iconica, pl. 29, figs. 79 a, b.
1958 *Acmaea fascicularis* Menke, Keen, Sea Shells of Tropical West America, p. 244.

Patella pallida Gould, 1859

Remarks—This Recent Japanese species is now recognised as belonging to the Acmaeidae.

Synonymy—

- 1859 *Patella pallida* Gould, Proc. Boston Soc. Nat. Hist., vol. 7, p. 162.
1952 *Tectura pallida* Gould, Kuroda & Habe, Check List Rec. Mar. Moll. Japan, p. 89.

Patella profunda Deshayes, 1863

Remarks—This Recent Reunion Island species is now known to belong to the Acmaeidae.

Synonymy—

- 1863 *Patella profunda* Deshayes, Moll. Réunion, p. 44, pl. 6, figs. 15, 16.
1942 *Patelloida profunda* Deshayes, Tonlin & Stephenson, Proc. Malac. Soc., London, vol. 25, p. 6.

Helcioniscus profundus var. *mauritiana* Pilsbry, 1891

Remarks—This Recent species and its variety from the island of Mauritius belong to the Acmaeidae.

Synonymy—

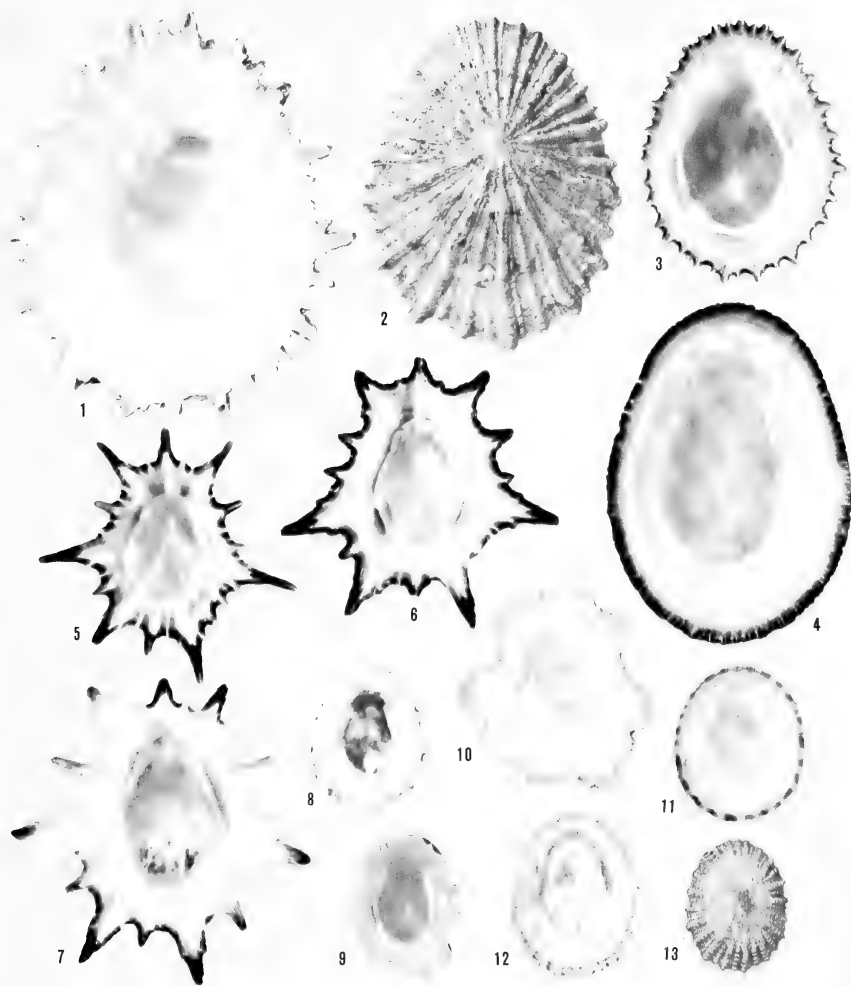
- 1891 *Helcioniscus profundus* var. *mauritiana* Pilsbry, 1891, Manual of Conchology, vol. 13, p. 150, pl. 65, figs. 97-99.

List of Recognized Taxa

SUBFAMILY **Patellinae**GENUS **Patella** Linnaeus, 1758Subgenus **Patella** Linnaeus, 1758*vulgata* Linnaeus, 1758. **Type.** Europe*aspera* Röding, 1798. Europe*depressa* Pennant, 1777. Europe*ferruginea* Gmelin, 1791. Mediterranean*baudonii* Drouet, 1858. Azores*rustica* Linnaeus, 1758. S. Europe-Mediterranean*piperata* Gould, 1846. Madeira and Cape Verde Ids.*caerulea* Linnaeus, 1758. Mediterranean, Portugal, Azores and Canary Ids.*moreleti* Drouet, 1858. Azores*lowei* d'Orbigny, 1839. Canary Ids.*gomesii* Drouet, 1858. Azores

Subgenus (not known)

candei d'Orbigny, 1839. Canary Ids.*citrullus* Gould, 1846. Madeira*concolor* Krauss, 1848. Natal and eastern South Africa*depsta* Reeve, 1855. St. Paul and Amsterdam Ids.*rangiana* Rochebrune, 1882. Cape Verde Ids.†*kaffraria* Rennie, 1930. Cretaceous, South AfricaSubgenus **Patellona** Thiele, in Troschel & Thiele, 1891*granatina* Linnaeus, 1758. **Type.** South Africa*oculus* Born, 1778. South Africa*adansonii* Dunker, 1853. West Africa*canescens* Gmelin, 1791. St. Helena*lugubris* Gmelin, 1791. West Africa and Cape Verde Ids.*plumbea* Lamarck, 1819. West Africa*safiana* Lamarck, 1819. Algeria to West AfricaSubgenus **Patellidea** Thiele, in Troschel & Thiele, 1891*granularis* Linnaeus, 1758. **Type.** South AfricaSubgenus **Cymbula** H. & A. Adams, 1854*compressa* Linnaeus, 1758. **Type.** South Africa*miniata* Born, 1778. South AfricaSubgenus **Olana** H. & A. Adams, 1854*cochlear* Born, 1778. **Type.** South AfricaSubgenus **Scutellastra** H. & A. Adams, 1854*argenvillei* Krauss, 1848. South Africa*barbara* Linnaeus, 1758. **Type.** South Africa*longicosta* Lamarck, 1819. South Africa*tabularis* Krauss, 1848. South Africa*exusta* Reeve, 1854. Mauritiussubsp. *pica* Reeve, 1854. Mauritius to Seychelles*flexuosa* Quoy & Gaimard, 1834. Indo-Pacific, Andamans to Tuamotussubsp. *optima* Pilsbry, 1927. Japan*kermadecensis* Pilsbry, 1894. Kermadec Ids.†*taurora* Fleming, 1973. Middle Oligocene, New Zealand*tucopiana* (Powell, 1925). Tikopia, Melanesia*laticostata* Blainville, 1825. south West Australia*peronii* Blainville, 1825. southern Australia*chapmani* Tenison Woods, 1875. South Australia to New South Wales†*hamiltonensis* (Chapman & Gabriel, 1923. Lower Pliocene, Australia†*cooperi* (Powell, 1938). Lower Miocene, New ZealandSubgenus **Ancistromesus** Dall, 1871*mexicana* Broderip & Sowerby, 1829. **Type.** West Mexico†*fuenzalidai* Herm, 1969. Pliocene, ChileGENUS **Helcion** Montfort, 1810Subgenus **Helcion** Montfort, 1810*pectunculus* (Gmelin, 1791). **Type.** South AfricaSubgenus **Ansates** Sowerby, 1839*pellucidus* (Linnaeus, 1758). **Type.** Western Europe? *tella* (Bergh, 1871). Sargasso SeaSubgenus **Patinastra** Thiele, in Troschel & Thiele, 1891*pruinosis* (Krauss, 1848). **Type.** South Africa*dunkeri* (Krauss, 1848). South AfricaSUBFAMILY **Nacellinae**GENUS **Cellana** H. Adams, 1869*eucosmia* (Pilsbry, 1891). Red Sea*radiata* (Born, 1778). India to Philippinessubsp. *capensis* (Gmelin, 1791). Natal to Zanzibarsubsp. *enneagona* (Reeve, 1854). Madagascar to Japansubsp. *orientalis* (Pilsbry, 1891). Indonesia; Japan; Marquesas†*deformis* (K. Martin, 1883). Miocene, Java*karachiensis* (Winckworth, 1930). Gulf of Oman to Karachi*livescens* (Reeve, 1855). **Type.** Mauritius*pricei* Powell, **new species.** Samoa and New Hebrides*garconi* (Deshayes, 1863). Reunion and Madagascar

Plate 65. *Patella* of the subgenus *Scutellastra*Figs. 1-3. *Patella* (*Scutellastra*) *barbara* Linnaeus, 1758.

Figs. 1, 3. Buluga Bay, East London, South Africa. Fig. 2. Port Alfred, South Africa.

Fig. 4. *Patella* (*Scutellastra*) *argenvillei* Krauss, 1848. Sea Point, South Africa.Figs. 5-7. *Patella* (*Scutellastra*) *longicosta* Lamarck, 1819. Kommetje, Cape Peninsula, South Africa.Figs. 8-9. *Patella* (*Scutellastra*) *flexuosa* Quoy & Gaimard, 1834. Fig. 8. Paia, Tahiti. Fig. 9. Wake Island.Fig. 10. *Patella* (*Scutellastra*) *flexuosa* subspecies *optima* Pilsbry, 1927. Waki, Satsuma, Japan; young example.Figs. 11-13. *Patella* (*Scutellastra*) *peronii* Blainville, 1825.

Fig. 11. Swansea, Tasmania. Figs. 12-13. Shellharbour, New South Wales, Australia.

(Cellana cont'd)

testudinaria (Linnaeus, 1758). Andaman Ids. to New Caledonia

vitiensis Powell, **new name**. Fiji

grata (Gould, 1859). Japan and Korea

mazatlanica (Sowerby, 1839). Japan and Ryukyu Ids.

nigrolineata (Reeve, 1854). Japan

toreuma (Reeve, 1855). Japan to Philippines

exarata (Reeve, 1854). Hawaiian Ids.

talcosa (Gould, 1846). Hawaiian Ids.

tahitensis (Pease, 1868). Tahiti and Pitcairn

ardosiaea (Hombron & Jacquinot, 1841). Juan Fernandez Id.

concliliata Iredale, 1940. Queensland

turbator Iredale, 1940. South Queensland

tramoserica (Holten, 1802). South Queensland to South Australia

solida (Blainville, 1825). Tasmania to South Australia

†*carpentariana* Skwarko, 1966. Lower Cretaceous, North Australia

†*cutdmorei* Chapman & Gabriel, 1923. Lower Miocene, Victoria

†*hentyi* Chapman & Gabriel, 1923. Lower Pliocene, Victoria

analogia Iredale, 1940. Lord Howe Id.

owensis Iredale, 1940. Lord Howe Id.

craticulata (Suter, 1905). Kermadec Ids.

denticulata (Marty, 1754). New Zealand

flava (Hutton, 1873). New Zealand

ornata (Dillwyn, 1817). New Zealand

radians (Gmelin, 1791). New Zealand

stellifera (Gmelin, 1791). New Zealand

strigilis (Hombron & Jacquinot, 1841). Auckland and Campbell Ids.

subsp. *bollonsi* Powell, 1955. Antipodes Ids.

subsp. *chathamensis* (Pilsbry, 1891). Chatham Ids.

subsp. *flemingi* Powell, 1955. Snares Ids.

subsp. *oliveri* Powell, 1955. Bounty Ids.

subsp. *redimiculum* (Reeve, 1854). Southern New Zealand

†*thomsoni* Powell & Bartrum, 1929. Lower Miocene, New Zealand

†*cophina* Powell, **new species**. Lower Miocene, New Zealand

taberna Powell, **new species**. Lower Miocene, New Zealand

GENUS *Nacella* Schumacher, 1817

Subgenus *Nacella* Schumacher, 1817

mytilina (Helbling, 1779). **Type**. Southern Chile to Kerguelen Id.

kerguelensis (E. A. Smith, 1877). Kerguelen and Heard Ids.

Subgenus *Patinigera* Dall, 1905

clypeator (Lesson, 1831). Chile

concinna (Strebel, 1908). South Georgia to Antarctica

deaurata (Gmelin, 1791). Patagonia, Falklands, Tierra del Fuego

subsp. *delicatissima* (Strebel, 1907). Magellan and Falklands

delesserti (Philippi, 1849). Marion Id.

edgari (Powell, 1957). Kerguelen Id.

flammea (Gmelin, 1791). Strait of Magellan

fuegiensis (Reeve, 1855). Magellan, Falklands, South Georgia

magellanica (Gmelin, 1791). **Type**. Magellan to Falklands

subsp. *venosa* (Reeve, 1854). Chiloe Island, Chile

macquariensis Finlay, 1927. Macquarie and Heard Ids.

terroris (Filhol, 1880). Campbell Id.

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[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Plate 66. *Patella* of the subgenus *Scutellastra*

Fig. 1. *Patella* (*Scutellastra*) *kermadecensis* Pilsbry, 1894. Raoul Island, Kermadec Islands. Largest living species of the subgenus.

Fig. 2. *Patella* (*Scutellastra*) *flexuosa* subspecies *optima* Pilsbry, 1927. Yakushima, Japan.

Figs. 3-4. *Patella* (*Scutellastra*) *laticostata* Blainville, 1825. Albany, Western Australia.

Fig. 5. *Patella* (*Scutellastra*) *tabularis* Krauss, 1848. Cape Point, South Africa.

Family Patellidae Rafinesque 1815

The Patellidae or family of true limpets have simple, oval to rounded, conical or cap-shaped shells, without a perforation, marginal notch or internal septum. They are characteristic of the intertidal zone and seldom extend much below low-tide mark. A detailed account of the animal, its habits, functions, distribution and geological range, is given in the introductory section of this work.

Subfamily Patellinae Rafinesque, 1815

The subfamily Patellinae includes the genera *Patella* and *Helcion*, as well as several subgenera of each.

The radula comprises four identical central teeth, often with the addition of a median central that may vary from vestigial to fully developed. The lateral is large and pluricuspid, and is flanked by three weak, slender, apparently functionless marginals. The radular ribbon is relatively short, straight, and folded back upon itself at the nascent end.

The gill cordon is continuous in all members, except in typical *Helcion*, which has the cordon interrupted by the head, understandable in that instance, since the sole species, *pectunculus*, has the anterior end reduced almost to nothing.

The shell in *Patella* is usually rather solid, porcellaneous within, and seldom iridescent. On the other hand, *Helcion* (*Patinastra*) is semitransparent, and *Cellana*-like, except for the dentition which closely resembles that of *Patella*.

The typical genus, *Patella*, is distributed along most of the eastern coast of Europe, from the Lofoten Islands, and including Britain, to Spain, the Mediterranean, west coast of Africa and offshore islands; also there is one species in Natal, and another, somewhat atypical, at the South Indian Ocean Islands of St. Paul and Amsterdam.

The subgenus *Patellona* is predominantly West African, but extends to South Africa; the subgenera *Cymbula* and *Olana* are exclusively South African; the subgenus *Scutellastra* is South African as well, but also has a very extensive Indo-Pacific range, and the subgenus *Ancistromesus*,

largest of all limpets, belongs exclusively to the west coast of Central America.

Numerous species, attributed to *Patella*, *Helcion* and *Nacella*, have been described from European Cretaceous and Tertiary horizons, but their true identity, of necessity based upon shell characters alone, is uncertain.

Genus *Patella* Linnaeus, 1758

Type: *Patella vulgata* Linnaeus, 1758

Shell ovate, conical or cap-shaped, with the apex subcentral, usually solid, and of medium size to very large. Sculpture consisting of radial ridges of varying strength, mostly crossed by concentric growth lines. Interior of shell varying from subtranslucent, polished and iridescent, to opaque porcellaneous. Colour pattern external, usually in the form of radials associated with the ribbing, and showing through to the interior in subtranslucent shells but confined to the marginal border in those with a thick porcellaneous internal layer.

The gill cordon is complete, and the radula relatively short and folded back upon itself at the nascent end. The radula formula is—

$$\begin{aligned} &3 + 1 + 4 + 1 + 3 \text{ or} \\ &3 + 1 + (2 + 1 + 2) + 1 + 3 \text{ or} \\ &3 + 1 + 5 + 1 + 3 \end{aligned}$$

The variations of the above formulae occur in the central teeth, which may consist of 4 identical centrals in a horizontal row, as in *Patella vulgata*, or in others when an incipient median central is added, or, again, in certain species of the subgenus *Scutellastra* when the median central attains the size of the other centrals, thus making 5 identical centrals. The lateral is almost invariably pluricuspid, and the 3 marginals are narrow, with very weak cusps at most, and they are apparently functionless.

The range of the genus is wide-spread in warm and temperate seas, but is absent from certain regions, notably both coasts of North America, the Caribbean and South America.

A number of fossil species attributed to *Patella* has been described, ranging from the upper Cretaceous onward, but most of these are difficult to assign generically or even to family since we lack knowledge of the soft parts.

The genus *Patella* is here divided into several subgenera that are each more or less restricted to definite geographical areas. Their synonymy is recorded under the relevant subgenera.

Subgenus *Patella* Linnaeus, 1758

Type: *Patella vulgata* Linnaeus, 1758

Shell of small to moderate size, the inner layer subtranslucent and more or less iridescent, often with the external colour pattern showing through the glaze. Gill cordon complete and radula with 4 identical central teeth, arranged in a horizontal row, and occasionally with an incipient median central, represented by a narrow functionless plate.

Distribution, the western coastline of Europe, from the Lofoten Islands, and including Britain, to the Mediterranean, down to Madeira and the Canary Islands, and appearing again along the coast of Natal.

Synonymy—

- 1758 *Patella* Linnaeus, Syst. Nat., ed. 10, p. 780. Type, by subsequent designation, Fleming, 1818: *Patella vulgata* Linnaeus, 1758.
 1810 *Patellus* Montfort, Conchyliologie Systématique, vol. 2, p. 67. Type, by original designation: *Patellus roseus* Montfort, 1810.
 1884 *Patellopsis* Thiele in Troschel, Das Gebiss der Schnecken, vol. 2, p. 324, based upon the radula (pl. 28, fig. 22) of an unnamed South African *Patella*, possibly *variabilis* Krauss, 1848.
 1884 *Patellastra* Monterosato, Natural. Sicil., vol. 3, p. 103. Type, by monotypy: *Patella lusitanica* Gmelin, 1791.
 1912 *Costatopatella* Pallary, Mem. Inst. Egypte, vol. 7 (3), p. 148.
 1920 *Granopatella* Pallary, Arch. Sci. Prot. Franc. Expl. Sci. Maroc, fasc. 2, p. 72.
 1920 *Laecipatella* Pallary, Arch. Sci. Prot. Franc. Expl. Sci. Maroc, fasc. 2, p. 72.

Patella vulgata Linnaeus, 1758

(Pl. 63, figs. 1-3; pl. 68, figs. 1, 2; pl. 61, fig. 1)

Range—Western Europe, Lofoten Islands to Spain and the British Isles.

Remarks—This is the common European edible limpet. It is moderately large, solid, oval and conical, radially ribbed, and usually whitish or yellowish, often radially lined or streaked in brown.

Description—Shell moderately large, up to 60 mm. (2½ inches) in length, solid, oval, conical, with the apex a little in front of the middle, and sculptured with radiating ribs and interstitial lirae. Colour varying from whitish to yellowish, sometimes radially lined or streaked with dark-brown. Interior weakly iridescent, the spatula grayish to leaden colour or clouded with whitish

callus, often with the shell margin dark-lined by the external pattern showing through.

Radula—Formula 3 + 1 + 4 + 1 + 3. The four central teeth are of approximately equal size, and are arranged in a straight horizontal line, without a median vestigial central.

Measurements (mm.)—

length	width	height	
60.5	53.0	32.0	Caldy Island, S. Wales
43.0	37.5	21.0	Isle of Man

Synonymy—

- 1758 *Patella vulgata* Linnaeus, Syst. Nat., ed. 10, p. 782.
 ? 1798 *Patella conus* Röding, Mus. Bolten., pt. 2, p. 8.
 1811 *Patella radiata* Perry, Conch., London, pl. 43, fig. 1 (non Born, 1778).
 1839 *Patella conica* Anton, Verzeichniss, p. 26 (non Blainville, 1825).
 1844 *Patella vulgata* var. *conica* Brown, Illust. Conch., ed. 2, p. 65.
 1844 *Patella vulgata* var. *communis* Brown, Illust. Conch., ed. 2, p. 63.
 1854 *Patella vulgata* Linn., Reeve, Conch. Iconica, vol. 8, pl. 18, figs. 42 a-c. (Dec.).
 1857 *Patella vulgata* var. *intermedia* Knapp (in Murray), Ann. Mag. Nat. Hist., 19, p. 211.
 1865 *Patella vulgata* var. *elevata* Jeffreys, Brit. Conch., vol. 3, p. 237.
 1865 *Patella vulgata* var. *picta* Jeffreys, Brit. Conch., vol. 3, p. 237.
 1887 *Patella vulgata* var. *secernenda* Dautzenberg, Excur. mal. St.-Lunaire, p. 13.
 1891 *Patella vulgata* Linn., Pilsbry, Man. Conch., vol. 13, p. 82, pl. 10, figs. 1-6.
 1906 *Patella vulgata* var. *aurea* Martel in Dautzenberg & Durouchoux, Suppl. Faun. malac. St.-Malo, p. 11.
 1906 *Patella vulgata* var. *major* Dautzenberg & Durouchoux, Suppl. Faun. malac. St.-Malo, p. 11.

Patella ferruginea Gmelin, 1791

(Pl. 69, figs. 1-3)

Range—Mediterranean, from the Aegean to Spain and North Africa.

Remarks—This species is easily recognised by its thick shell, strong radial ribs, deeply corrugated margin and ashen colour.

Description—Shell moderately large, up to 62 mm. (2.7/16 inches) in length, very solid, ovate, conical, with the apex subcentral, coarsely sculptured with numerous strong radial ribs, that are rendered scabrous by concentric growth lines, and also strongly corrugate the margin. Colour, externally dull ashen, more or less stained with pale brown; internally, bluish white, corrugated margin bordered in dark-brown, almost black, and the spatula clouded with whitish callus.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Radula very similar to that of *caerulea*, except that the

small slender median central is a definite tooth bearing a small cusp.

Measurements (mm.)—

length	width	height	
60.0	51.5	24.0	Corsica
59.0	47.0	21.0	Corsica

Synonymy—

- 1791 *Patella ferruginea* Gmelin, Syst. Nat., ed. 13, p. 3706; based upon Martini-Chemnitz, Conch. Cab., vol. 1, pl. 8, fig. 66.
 1819 *Patella luteola* Lamarck, Anim. sans vert., vol. 6 (1), p. 327.
 1819 *Patella pyramidata* Lamarck, Anim. sans vert., vol. 6 (1), p. 327.
 1826 *Patella rouxii* Payraudeau, Cat. Moll. Corse, p. 90.
 1826 *Patella lamarckii* Payraudeau, Cat. Moll. Corse, p. 90.
 1854 *Patella costoso-plicata* Reeve, Conch. Iconica, vol. 8, pl. 8, figs. 14 a, b.
 1884 *Patella ferruginea* var. *ficarazzensis* de Gregorio, Bull. Soc. Mal. Ital., vol. 10, pp. 120-124.
 1884 *Patella ferruginea* var. *imperatoria* de Gregorio, Bull. Soc. Mal. Ital., vol. 10, pp. 120-124.
 1884 *Patella ferruginea* var. *percostata* de Gregorio, Bull. Soc. Mal. Ital., vol. 10, pp. 120-124.
 1884 *Patella ferruginea* var. *sitta* de Gregorio, Bull. Soc. Mal. Ital., vol. 10, pp. 120-124.
 1891 *Patella ferruginea* Gmelin, Pilsbry, Man. Conch., vol. 13, p. 81, pl. 53, figs. 1-3; pl. 17, figs. 23, 24.
 1950 *Patella luteola* Lamarck, Mermod, Rev. Suisse Zool., vol. 57, no. 34, p. 692, fig. 3 (type).
 1968 *Patella ferruginea* Gmelin, Nordseeck, Eur. Meeres-Gehäuseschn. Stuttgart, p. 15.

Records—CORSICA; near Bonifacio (AWBP. coll. 28388). SPANISH MOROCCO; Melilla (AWBP. coll.); Chafarinas Islands (Zafarines), 35° 10' N., 2° 25' E. (AWBP. coll.).

Types—The type of *luteola* is in the Museum d'Histoire Naturelle de Geneve.

***Patella baudonii* Drouet, 1858**

(Pl. 75, figs. 1, 2)

Range—Azores, Santa Maria and Pico.

Remarks—This species, which the writer has not seen, seems to be closely allied to, if not identical with, *Patella ferruginea* Gmelin, 1791. Pilsbry's translation of the original description follows, and the illustrations are from Drouet's original figures.

Description—"Shell large, subelevated, coarsely ribbed, plicate, solid, thick; outside greyish-green, inside white; vertex subacute, submedian; aperture oval, a little crenated."

Measurements (mm.)—

length	width	height	
60.0	50.0	25.0	(Drouet)

Synonymy—

- 1858 *Patella baudonii* Drouet, Moll. Mar. Açores, p. 41, pl. 2, figs. 8, 9.
 1891 *Patella baudonii*: Pilsbry, Man. Conch., vol. 13, p. 86, pl. 54, figs. 15, 16.

***Patella rustica* Linnaeus, 1758**

(Pl. 69, figs. 4, 5)

Range—Atlantic coast of south west France, Portugal, Spain, Mediterranean and Adriatic Seas.

Remarks—This species, better known by the Gmelin name, *lusitanica*, is rather small, ovate-conical, and densely sculptured with fine granular radials. The external colour is greyish, or pale brownish, speckled with black, and internally it is broadly radially banded in dark purplish-brown. A nearly related species is the narrowly-ovate *piperata* from Madeira and the Cape Verde Islands.

Description—Shell rather small, up to 35 mm. (1½ inches) in length, solid, ovate, tall-conical, with the apex slightly anterior to the middle. Sculpture consisting of very numerous, closely spaced, narrow, somewhat uneven, granulose radial riblets. Colour, externally pale yellowish-brown to greyish, often with the rib-granules black, internally broadly rayed in dark-brown or blue-black on a greyish-silvery ground. Spatula white callused, often surrounded by a yellowish-brown stain.

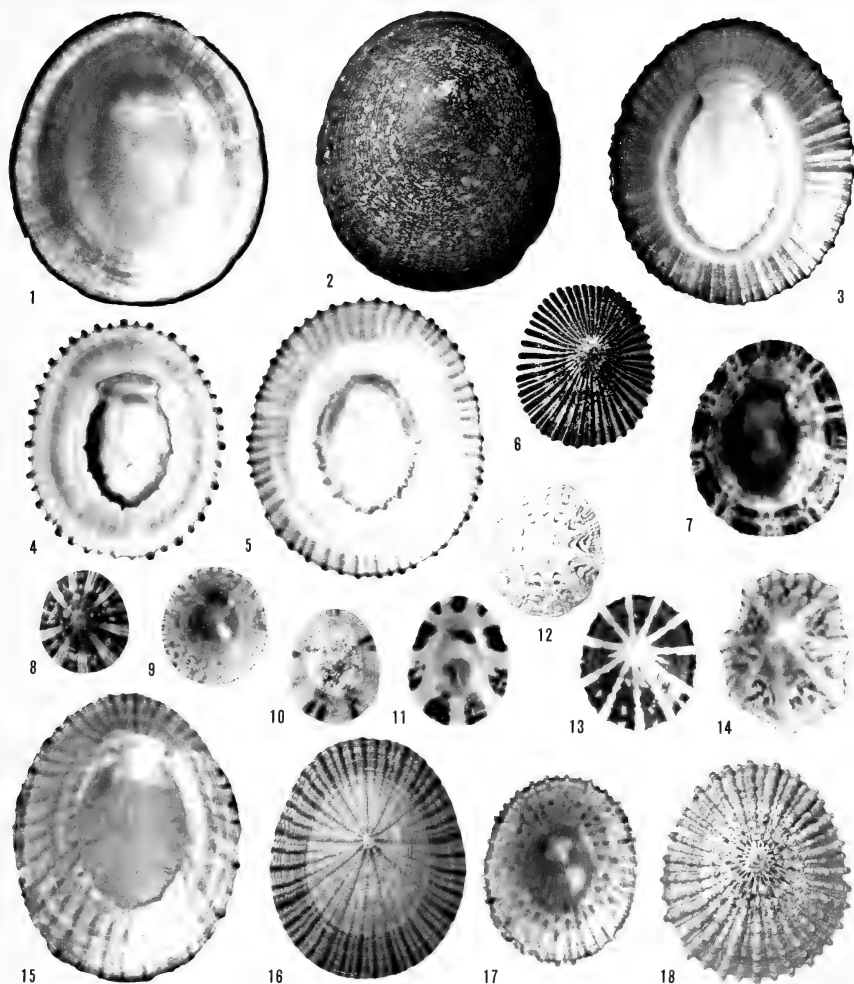
Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Radula with or without a narrow median central tooth, remaining four centrals of uniform size, and arranged in a horizontal line.

Measurements (mm.)—

length	width	height	
35.0	28.5	17.0	Melilla, Morocco
28.0	24.0	12.5	Melilla, Morocco

Synonymy—

- 1758 *Patella rustica* Linnaeus, Syst. Nat., ed. 10, p. 783.
 1791 *Patella lusitanica* Gmelin, Syst. Nat., ed. 13, p. 3715.
 1798 *Patella squamata* Röding, Mus. Bolten, pt. 2, p. 10.
 1819 *Patella punctata* Lamarck, Anim. sans vert., vol. 6, p. 333.
 1825 *Patella subgranularis* Blainville, Dict. Sci. Nat., vol. 38, p. 113. (fide Christiaens, 1968, p. 367).
 1854 *Patella nigro-punctata* Reeve, Conch. Iconica, vol. 8, pl. 23, figs. 57 a-c (Dec.).
 1883 *Patella lusitanica* var. *minor* Marion, Faune bass. med., p. 48.
 1884 *Patella lusitanica* Gmel., Monterosato, Natural. Sicil., vol. 3, p. 103.
 1891 *Patella lusitanica* Gmel., Thiele, in Troschel & Thiele, Das Gebiss der Schnecken, 2, pl. 28, fig. 12 (radula).
 1891 *Patella lusitanica* Gmel., Pilsbry, Man. Conch., vol. 13, p. 87, pl. 11, figs. 15-19.
 1912 *Patella rustica* Linne' var. *major* Pallary, Explor. scient. Maroc., p. 72.

Plate 67. Indo-Pacific *Cellana*

Figs. 1, 2. *Cellana testudinaria* (Linnaeus, 1758). Vanualava, Banks Islands.

Fig. 3. *Cellana talcosa* (Gould, 1846). Molokai, Hawaiian Islands.

Figs. 4-6. *Cellana exarata* (Reeve, 1854). Molokai, Hawaiian Islands.

Fig. 7. *Cellana grata* (Gould, 1859). Matsushima Island, Korea.

Figs. 8, 9. *Cellana radiata* (Born, 1778). Colombo, Ceylon.

Figs. 10, 11. *Cellana radiata* subspecies *capensis* (Gmelin, 1791). Near Durban, Natal.

Figs. 12, 13. *Cellana radiata* subspecies *orientalis* (Pilsbry, 1891). Fig. 12. Russell Islands, Solomon Islands (note the strong radial folds). Fig. 13. Tau Island, Samoa.

Fig. 14. *Cellana radiata* subspecies *emiragona* (Reeve, 1854). Jolo, Philippine Islands.

Figs. 15, 16. *Cellana nigrolineata* (Reeve, 1854). Fig. 15. Fukura, Awaji, Japan. Fig. 16. Chirigashima, Japan.

Figs. 17, 18. *Cellana mazatlantica* (Sowerby, 1839). Bonin Islands.

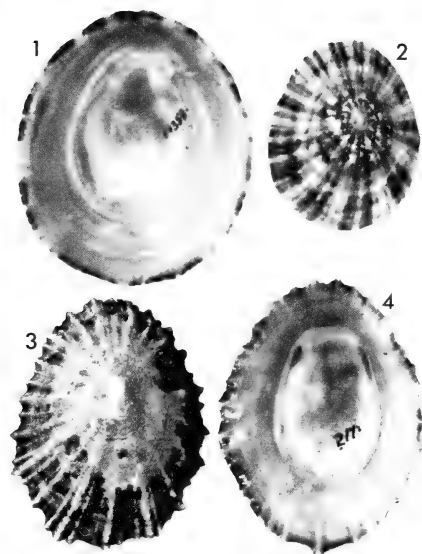


Plate 68. Figs. 1, 2. *Patella vulgata* Linnaeus, 1758. Fig. 1. Kimmeridge, England, 52 mm., AWBP coll. 11358. Fig. 2. Isle of Man, 38 mm., AWBP coll. 11359. Figs. 3, 4. *Patella aspera* Röding, 1798, Caldy Island, Wales, 47 mm., AWBP coll. 217.

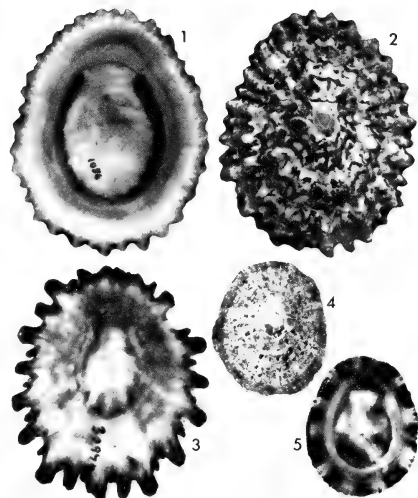


Plate 69. Figs. 1-3. *Patella ferruginea* Gmelin, 1791. Fig. 1. Chafarines Islands, Morocco, 55 mm., AWBP coll. 1054. Fig. 2. Bonifacio, Corsica, 60 mm., AWBP coll. 28388. Fig. 3. Melilla, Morocco, 42 mm., AWBP coll. 30974. Figs. 4, 5. *Patella rustica* Linnaeus, 1758, Oran, Algeria, 25-26 mm., AWBP coll. 80.

- 1912 *Patella rustica* Linné var. *maroccana* Pallary, Explor. scient. Maroc., p. 72.
 1938 *Patella lusitanica* var. *orientalis* Pallary, Jour. Conchyl., vol. 82, p. 47.
 1950 *Patella punctata* Lam., Mermod. Rev. Suisse Zool., vol. 57 (34), p. 695, fig. 7 (type).
 1968 *Patella lusitanica* Gmelin, Christiaens, Bull. Mus. Nat. d'Hist. Nat., ser. 2, vol. 40 (2), pp. 366, 367.
 1968 *Patella (Patellastra) rustica* L., Nordsieck, Die europ. Meeres Gehäuseschnecken, Stuttgart, p. 15.

Patella piperata Gould, 1846

(Pl. 71)

Range—Madeira and Cape Verde Islands.

Remarks—Shell very similar to that of *rustica* in sculpture and in coloration, but more elongate-ovate in its younger stages, and with the apex nearer to the anterior end.

Radula—The radula differs from that of *rustica* in that the four central teeth are not in horizontal alignment, the middle pair being set lower than the outer pair (Christiaens, 1968, p. 370, fig. 2a).

Measurements (mm.)—

length	width	height	
44.0	40.0	—	Christiaens, 1968, p. 372
27.0	21.0	12.0	Madeira

Synonymy—

- 1839 *Patella guttata* Orbigny, in Webb & Berthelot, Hist. Nat. Moll. Canaries, p. 98 (non Gmelin, 1791).
 1846 *Patella piperata* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 150.
 1846 *Patella nigroquamosa* Dunker, Zeitschr. f. Malak., p. 25.
 1866 *Patella frauenfeldi* Dunker, Verh. k. k. zool.-bot. Ges. Wien, vol. 16, p. 914. "Madrass" in error for Madeira.
 1867 *Patella frauenfeldi* Dunker, Frauenfeld, Reise Novara, Zool., vol. 2, pt. 3, Moll., p. 15, pl. 2, figs. 26 a, b.
 1968 *Patella piperata watsoni* Christiaens, Bull. Mus. Nat. d'Hist. Nat. ser. 2, vol. 40, no. 2, p. 371, text fig. 2 b; pl. 1, fig. b.
 1968 *Patella piperata nigro-radiata* Christiaens, Bull. Mus. Nat. d'Hist. Nat. ser. 2, vol. 40, no. 2, p. 371, text fig. 2 c; pl. 1, fig. c.
 1968 *Patella piperata alba* Christiaens, Bull. Mus. Nat. d'Hist. Nat. ser. 2, vol. 40, no. 2, p. 371, pl. 1, fig. g (non *P. alba* Anton, 1839).

Patella caerulea Linnaeus, 1758

(Pls. 61, 63, 72, 74)

Range—Mediterranean and Adriatic Seas, Portugal, Azores, Madeira and Canary Islands.

Remarks—This species is variable in shape, colour, and strength of the radial ribbing, but in general terms it is a depressed, thin, and spreading shell, with 6 or 7 distinct marginal angles, resultant from 7 to 9 prominent radial folds. The typical form of the species from the Mediterranean and Adriatic Seas, has a colour range, varying from almost white to buff or pale brownish, often radially banded with iridescent blue.

Shells from the Azores and Madeira are larger, even more depressed than the typical species, have broader and more prominent radial folds, and are of much darker colour, being dark reddish brown externally, similarly coloured internally, but diffused with iridescent blue, and with a distinct-edged, white spatula. This latter form is *crenata* Gmelin, and when more material is studied, Gmelin's name may prove to be usable to define a regional subspecies of *caerulea*, restricted to the Azores, Madeira and Canary Islands. Negating this possibility is the fact that shells from the adjacent mainland of Spanish Morocco have the dark colouring of *crenata* but a shape and sculpture similar to those in typical *caerulea*.

Description—Shell of moderately large size, 40-71 mm. (1½-2¾ inches) in length, thin, depressed, usually distinctly 6 or 7 angled, resultant from 7 to 9 broadly rounded primary folds that project at the margin. Surface crowded with secondary radials of varying sizes, mostly imbricated by concentric growth lines. Colour whitish or buff externally, the interior silvery-white, radially lined or banded in blue, the spatula bluish or white-callused. Some examples have a pale yellowish interior without radial markings, and the form *crenata* is dark reddish brown, internally diffused with iridescent blue, and with a clear-cut white spatula.

Radula—Formula $3 + 1 + (2+X+2) + 1 + 3$. The radula is of the same style as that of *vulgata*, except for a slight median gap between the pairs of four centrals, in which appears a narrow vestigial plate. The four functional centrals, as in *vulgata*, are in a straight horizontal row.

Measurements (mm.)—(all A. W. B. Powell collection.)

length	width	height	
51.0	46.0	12.0	Capri, Italy
36.0	30.0	10.5	Melilla, Morocco
71.0	64.0	14.0	Madeira (<i>crenata</i> form)

Synonymy—

- 1758 *Patella caerulea* Linnaeus, Syst. Nat., ed. 10, p. 782.
 1791 *Patella crenata* Gmelin, Syst. Nat., ed. 13, p. 3706.
 1791 *Patella margaritacea* Gmelin, Syst. Nat., ed. 13, p. 3707.
 1793 *Patella tarentina* von Sahlb., Reise ins. Koenig. Neapel, p. 359, pl. 6, fig. 2.
 1798 *Patella silicina* Röding, Mus. Bolten., pt. 2, p. 9.
 1819 *Patella tarentina* Lamarck, Anim. sans vert., vol. 6, p. 332.
 1826 *Patella bonnardii* Payraudeau, Moll. de Corse, p. 89.
 1836 *Patella fragilis* Philippi, Enum. Moll. Sicil., vol. 1, p. 110.
 1838 *Patella subplana* Potiez & Michaud, Gal. Moll. Douai, vol. 1, p. 524.
 1854 *Patella scutellaris* Lam., Reeve, Conch. Iconica, vol. 8, pl. 20, fig. 49.
 1882 *Patella stellata* Bucquoy, Dautzenberg & Dollfus, Moll. mar. Roussillon. (non Helbling, 1779).
 1882 *Patella adpersa* Bucquoy, Dautzenberg & Dollfus, Moll. mar. Roussillon.
 1882 *Patella caerulea* var. *cognata* Bucquoy, Dautzenberg & Dollfus, Moll. mar. Roussillon, p. 471.
 1882 *Patella caerulea* var. *intermedia* Bucquoy, Dautzenberg & Dollfus, Moll. mar. Roussillon, p. 471.
 1891 *Patella caerulea* Linneé, Pilsbry, Man. Conch., vol. 13, p. 83, pl. 10, figs. 7-12.
 1950 *Patella tarentina* Lam., Mermod, Rev. Suisse Zool., vol. 57 (34), p. 695 (text figs. of type series).

Records—ITALY: Naples; Isle of Capri; Palermo, Sicily. MALTA. MOROCCO: Melilla. MADEIRA (*crenata* form). (All AWBP coll.)

Patella moreleti Drouet, 1858

(Pl. 75, figs. 3, 4)

Range—Fayal, Azores.

Remarks—The writer has not seen this species which possibly may be only a form of *Patella caerulea* Linnaeus. Pilsbry's translation of the original description follows, accompanied by copies of Drouet's figures.

Description—"Shell subdepressed, very rugose, ribbed, the ribs scaly, scarcely solid; brownish-green outside; inside brownish or reddish, iridescent, with a white spot at the summit. Apex acute. Aperture ovate, crenulated."

Measurements (mm.)—

length	width	height	
40.0	30.0	12.0	(Drouet)

Synonymy—

- 1858 *Patella moreleti* Drouet, Moll. Mar. Açores, p. 42, pl. 2, figs. 10, 11.
 1891 *Patella moreleti* Drouet, Pilsbry, Man. Conch., vol. 13, p. 85, pl. 56, figs. 27, 28.

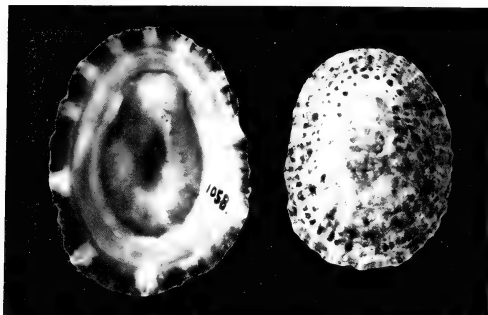


Plate 71. *Patella piperata* Gould, 1846. Madeira, 27 mm., AWBP coll. 1058.

Patella lowei Orbigny, 1839

(Pl. 74, figs. 1, 2)

Range—Canary Islands.

Remarks—This species appears to be closely allied to the Mediterranean *caerulea*, from which it differs mainly in having stronger, and more regular sculpture, resulting in a more even denticulation of the margin, as opposed to the 6 or 7 distinct marginal angles of *caerulea*. Also, the coloration in *lowei* is darker, the exterior being rusty-brown, and the interior dark bluish to reddish brown at the edges, reflecting iridescent blue, and always with a clearcut white spatula.

Description—Shell of moderate size, up to 56.5 mm. (2¼ inches) in length, ovate, depressed, with the apex towards the anterior third, solid but not very thick, densely sculptured with broadly rounded primary radials and narrow intermediates. The margin is strongly and regularly corrugated, the projections compound and foliated. Colour as described above.

Measurements (mm.)—(both A. W. B. Powell collection).

length	width	height	
56.5	48.0	13.0	Teneriffe
54.5	44.5	11.0	Teneriffe

Synonymy—

- 1839 *Patella lowei* Orbigny, in Webb and Berthelot, Hist. Nat. Canaries, Moll., vol. 2, p. 97, pl. 7, figs. 9, 10.
 1839 *Patella azorica* Nuttall, in Jay, Cat. Shells, ed. 3, p. 38.
 1891 *Patella caerulea* var. *lowei* Orbigny, Filsbry, Man. Conch., vol. 13, p. 84, pl. 29, figs. 44-46; pl. 53, figs. 7-11.

Records—CANARY ISLANDS (Orbigny); Teneriffe (AWBP coll. 5268).

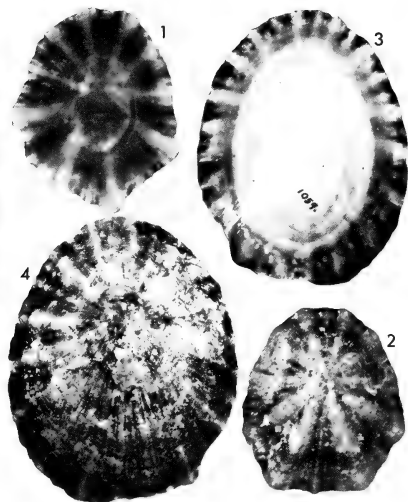


Plate 72. Figs. 1, 2. *Patella caerulea* Linnaeus, 1758. Isle of Capri, Italy, 51 mm., AWBP coll. 211. Figs. 3, 4. *Patella sahana* Lamarck, 1819. Oran, Algeria, 65 mm., AWBP coll. 1959.

Patella gomesii Drouet, 1858

(Pl. 74, figs. 5, 6)

Range—Azores, Bay of San Lourenzo, Santa Maria and Pico.

Remarks—The writer has not seen examples of this shell, which may prove to be a form of *lowei*. Its distinctive character is in having about 14 very prominent rounded radial folds, the whole surface, folds included, being densely radially lirate.

Description—(Pilsbry's translation of original): "Shell large, subdepressed, rugose, ribbed-plicate, rather solid; outside grayish-brown or rufescent; inside shining, brown, pearly; apex situated at the front third of the length, obtuse; aperture oval, entire."

Measurements (mm.)—

length	width	height
50-60	50-53	12-15

Synonymy—

- 1858 *Patella gomesii* Drouet, Moll. Mar. Iles Açores, p. 39, pl. 1, figs. 6, 7.
 1891 *Patella gomesii* Drouet, Filsbry, Man. Conch., vol. 13, p. 86, pl. 54, figs. 17, 18.

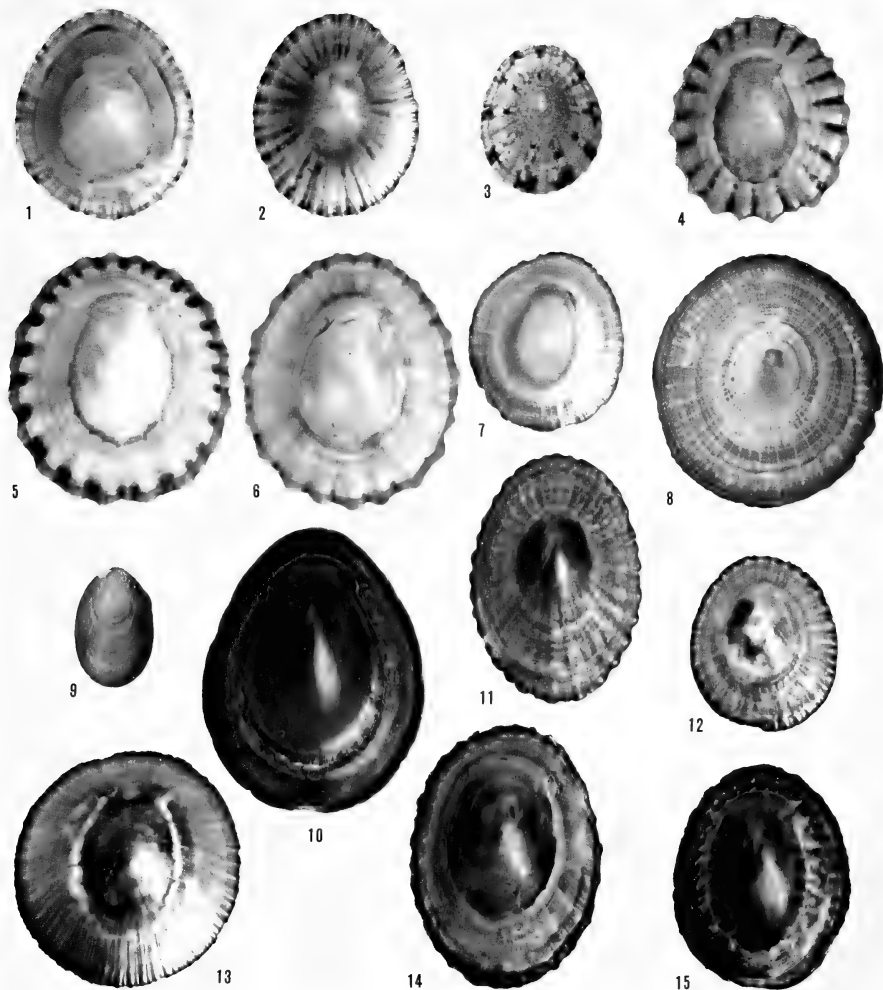


Plate 73. Antarctic Australian *Cellana* and
Subantarctic *Nacella*

(for plate 70, see p. 105)

Figs. 1-3. *Cellana tramoserica* (Holten, 1802). Fig. 1. South Australia. Fig. 2. Caloundra, Queensland. Fig. 3. Torquay, Victoria.

Figs. 4-6. *Cellana solida* (Blainville, 1825). Figs. 4, 5. Stanley, Tasmania. Fig. 6. South Australia (*rubraurantiaca* form).

Figs. 7, 8. *Cellana ardosiaea* (Hombron & Jacquinot, 1841). Island of Juan Fernandez.

Fig. 9. *Nacella mytilina* (Helbling, 1779). Falkland Islands.

Fig. 10. *Nacella kerguelensis* (E. A. Smith, 1877). Heard Island.

Fig. 11. *Nacella (Patinigera) deaurata* (Gmelin, 1791). Falkland Islands.

Fig. 12. *Nacella (Patinigera) terroris* (Filhol, 1880). Campbell Island.

Fig. 13. *Nacella (Patinigera) clypeator* (Lesson, 1831). Chile.

Figs. 14, 15. *Nacella (Patinigera) magellanica* (Gmelin, 1791). Possession Bay, Patagonia.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus Uncertain

The following six species of *Patella* are insufficiently understood, particularly with regards to their soft anatomy, to be assigned as yet to their proper subgenera.

Patella candei Orbigny, 1839

(Pl. 75, figs. 7, 8)

Range—Canary Islands.

Remarks—The writer has not seen this species, but from published information it appears to be closely allied to *citrullus* from Funchal, Madeira. The surface has subobsolete radials crossed by prominent wavy concentric lirations that haphazardly anastomose to form an irregular netted appearance.

Description—(Pilsbry's 1891 translation of the original description): "Shell elevated, conical, thick, smooth or irregularly roughened; ovate, margin entire. Inside buff, bluish in the middle, outside pale yellow."

Measurements (mm.)—

length	width	height
67.0	58.0	27.0

Synonymy—

- 1839 *Patella candei* Orbigny, in Webb and Berthelot, Hist. Nat. Canaries, vol. 2, Moll., p. 98, pl. 7, figs. 11, 12.
 1854 *Patella candei* Orbigny, Reeve, Conch. Iconica, vol. 8, pl. 15, figs. 34 a, b.
 1891 *Patella candei* Orbigny, Pilsbry, Man. Conch., vol. 13, p. 86, pl. 55, figs. 22-24.

Patella citrullus Gould, 1846

(Pl. 75, figs. 9, 10)

Range—Funchal, Madeira.

Remarks—The writer has not seen examples of this species which appears to be related to *candei*. Pilsbry (1891, l.c.) remarked that the external surface resembles the skin of a cucumber.

Description—(original) "Shell sub-diaphanous, thin sub-conical, moderately elevated, summit prominent; apex anterior, acute, feebly incurved, usually somewhat eroded; a great number of faintly

elevated lines, studded with fine tubercles or asperities, radiate from it, and become obsolete about half way towards the margin. Striae of increment coarse and irregular, overlaying each other, so as to give the shell a rude, concentrically squamose aspect externally; disc nearly oval, a little narrowed anteriorly; margin very thin and sharp, finely and irregularly undulated. External colour a dusky olive-green, with a shade of brown showing through it, ornamented with concentric, undulating lines of obscure white. Interior greenish-white, with bright iridescent reflections; a slight spatulaform deposit at the fundus, bluish at the edges and forepart, passing into greenish towards the middle and posterior portions."

Measurements (mm.)—

length	width	height
45.0	32.0	7.0

Synonymy—

- 1846 *Patella citrullus* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 149.
 1891 *Patella citrullus* Gould, Pilsbry, Man. Conch., vol. 13, p. 86, pl. 28, figs. 39-41.
 1964 *Patella citrullus* Gould, Johnson, U. S. Nat. Mus. Bull. 239, p. 56.

Patella concolor Krauss, 1848

(Pls. 64, 76, 78)

Range—Natal coast to as far south and west as Bushman's River, near Port Elizabeth.

Remarks—The former name of this well-known South African limpet, *Patella variabilis* Krauss, 1848, is invalidated by two prior homonyms, those of Roding, 1798, and Risso, 1826. The earliest valid name to replace *variabilis* is *concolor* which is the uniformly dark-ashen colour form of this species. The species is exceedingly variable in colour pattern, but the shape, which is ovate, distinctly narrowed in front, remains constant. Also it is of light build and is often semi-transparent.

Description—Shell rather small, usually between 30 and 35 mm. in length, but occasionally attaining 50 mm. (2 inches) in length, of light build, sometimes semi-transparent, rather depressed, ovate, but distinctly narrowed at the anterior end. Sculptured with about 80 fine but somewhat unequal radial ribs, crossed by dense inconspicuous concentric lirae. Apex subcentral to about the anterior third, the area in its vicinity usually smooth. Colour extremely variable, ranging from plain yellow, pale yellowish brown, and rusty-brown (*concolor*) to almost black, and variously maculated; sometimes the

yellow form has one, or several, dark-brown radial streaks, and the black form (*polygramma*) has the primary radials picked out in white; the common form is pale yellowish brown, radially lined and speckled in dark-brown; spatula ill-defined, light brownish or clouded with white callus.

Radula—Formula $3 + 1 + (2+0+2) + 1 + 3$. The radula differs from those of all other South African patellids in the absence of the middle member of the central teeth; the four remaining centrals, however, are grouped in pairs with a space between them, whereas in the radula of *Patella vulgata* and other European patellids, the four centrals are closely grouped, without space for a middle member.

Measurements (mm.)—

length	width	height	
50.0	45.0	11.25	South Africa
48.5	41.25	14.00	Natal coast
35.0	30.5	9.00	Port Alfred
28.5	24.0	7.00	Coffee Bay

Synonymy—

- 1848 *Patella variabilis* Krauss, Sudafr. Moll., Stuttgart, p. 55, pl. 3, fig. 12 (non *P. variabilis* Risso, 1826).
 1848 *Patella variabilis* var. *fasciata* Krauss, Sudafr. Moll., Stuttgart, p. 55, pl. 3, fig. 12 a (non *P. fasciata* Gmelin, 1791).
 1848 *Patella variabilis* var. *radiata* Krauss, Sudafr. Moll., Stuttgart, p. 55, pl. 3, fig. 12 b. (non *P. radiata* Born, 1778).
 1848 *Patella variabilis* var. *concolor* Krauss, Sudafr. Moll., Stuttgart, p. 55, pl. 3, fig. 12 c.
 1891 *Helcioniscus variabilis* Krauss, Pilsbry, Man. Conch., vol. 13, p. 147, pl. 16, figs. 18-20.

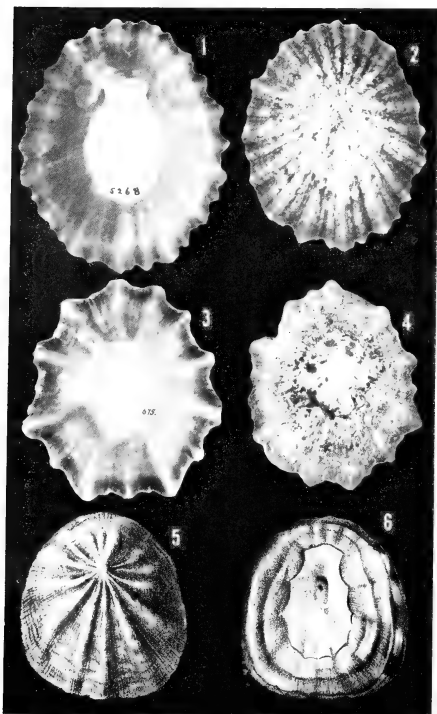


Plate 74. Figs. 1, 2. *Patella lowei* d'Orbigny, 1839, Teneriffe, Canary Islands, 56.5 mm., AWBP coll. 5268. Figs. 3, 4. *Patella* cf. *caerulea* Linnaeus, 1758 (*crenata* form), Madeira, 70 mm., AWBP coll. 675. Figs. 5, 6. *Patella gomesii* Drouet, 1858, Azores, 50-60 mm. From Pilsbry, 1891, pl. 54, figs. 17, 18.

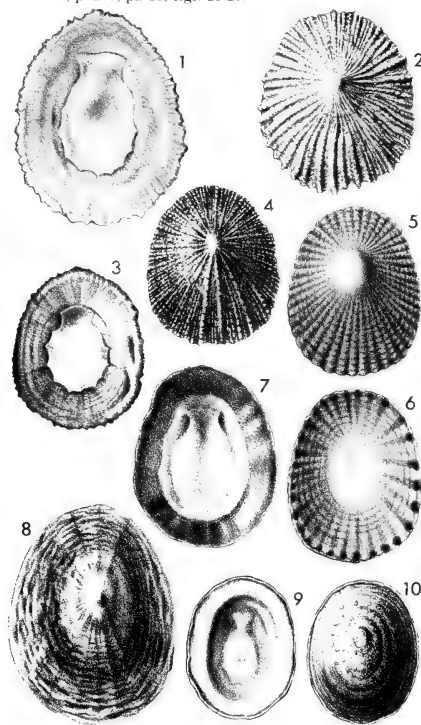
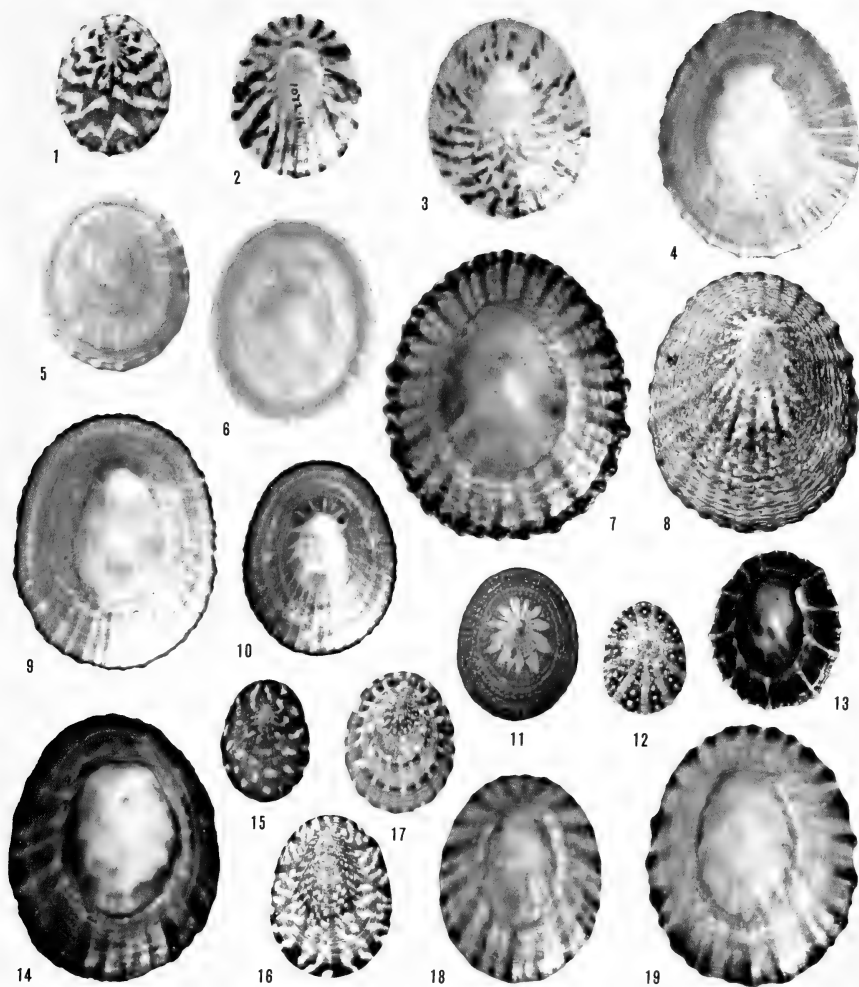


Plate 75. Figs. 1, 2. *Patella baudonii* Drouet, 1858, Azores, 60 mm. Figs. 3, 4. *Patella moreleti* Drouet, 1858, Fayal, Azores, 40 mm. Figs. 5, 6. *Patella rangiana* Rochebrune, 1882, Cape Verde Islands, 44 mm. Figs. 7, 8. *Patella candei* d'Orbigny, 1839, Canary Islands, 67 mm. Figs. 9, 10. *Patella citrullus* Gould, 1846, Funchal, Madeira, 45 mm. (All figures from Pilsbry, 1891, Manual of Conchology, vol. 13, plates 45, 54, 55, 56 and 58).

Plate 70. New Zealand *Cellana*

(for plate 73, see p. 101)

Figs. 1-4. *Cellana radians* (Gmelin, 1791). Fig. 1. Mount Maunganui, Bay of Plenty (earlier pattern). Figs. 2, 3. Motutahi Island, Auckland. Fig. 4. Herekopare Island, Stewart Island (perana form).

Figs. 5, 6. *Cellana flava* (Hutton, 1873). Fig. 5. East Cape. Fig. 6. Cape Campbell, Marlborough.

Figs. 7, 8. *Cellana denticulata* (Marty, 1784). Mount Maunganui, Bay of Plenty.

Figs. 9-11. *Cellana stellifera* (Gmelin, 1791). Fig. 9. Whan-

garei Heads. Fig. 10. Ti Point, Hauraki Gulf. Fig. 11. Long Beach, Bay of Islands (bleached coloration of beach shells).

Figs. 12, 13. *Cellana ornata* (Dillwyn, 1817). Fig. 12. Motutara, West Coast, Auckland. Fig. 13. Mount Maunganui.

Figs. 14-16. *Cellana strigilis* (Hombron & Jacquinot, 1841). Campbell Island.

Figs. 17-19. *Cellana strigilis* subspecies *redimiculum* (Reeve, 1854). Kartigi Beach, North Otago, South Island, New Zealand.

- 1921 *Patella variabilis constellata* G. B. Sowerby, Proc. Malac. Soc. Lond., vol. 14, p. 127.
- 1931 *Patella variabilis* Krauss, Tomlin, Ann. Natal Mus., vol. 6 (3), p. 417.
- 1931 *Patella variabilis fasciolata* Tomlin, Ann. Natal Mus., vol. 6 (3), p. 418; nom. nov. pro *P. variabilis fasciata* Krauss, 1848 (non Gmelin, 1791).
- 1931 *Patella variabilis polygramma* Tomlin, Ann. Natal Mus., vol. 6 (3), p. 418; nom. nov. pro *P. variabilis radiata* Krauss, 1848 (non Born, 1778).
- 1932 *Patella variabilis* Krauss, Turton, Mar. Shells Port Alfred, p. 167, sp. 1187.
- 1932 *Patella variabilis fasciata* Krauss, Turton, Mar. Shells Port Alfred, p. 167, sp. 1188.
- 1932 *Patella variabilis radiata* Krauss, Turton, Mar. Shells Port Alfred, p. 167, sp. 1189.
- 1932 *Patella variabilis concolor* Krauss, Turton, Mar. Shells Port Alfred, p. 168, sp. 1190.
- 1932 *Patella variabilis constellata* Sby., Turton, Mar. Shells Port Alfred, p. 168, sp. 1191.
- 1932 *Patella variabilis helvola* Turton, Mar. Shells Port Alfred, p. 168, sp. 1192.
- 1932 *Patella rietensis* Turton, Mar. Shells Port Alfred, p. 167, pl. 38, fig. 1183.
- 1932 *Patella rota* (non Gmelin, 1791) Turton, Mar. Shells Port Alfred, p. 168, sp. 1193.
- 1932 *Patella helena* Turton, Mar. Shells Port Alfred, p. 168, pl. 39, fig. 1194.
- 1932 *Patella conspicua* (non Philippi, 1849) Turton, Mar. Shells Port Alfred, p. 168, sp. 1196 (in part).
- 1932 *Patella farquhari* Turton, Mar. Shells Port Alfred, p. 170, pl. 40, fig. 1207.
- 1949 *Patella variabilis* Krauss, Koch, Ann. Natal Mus., vol. 11 (3), p. 510, pl. 23, figs. 1-11; text figs. 21, 22 (radula).

Records—SOUTH AFRICA: Natal coast to as far south and west as Port Elizabeth (Koch, 1949); Natal (ex Koch; AWBP coll.); Umtwalumi, 22 miles N. of Port Shepstone (V. Orr, 1955; ANSP); Port St. John's Pondoland (V. Orr; ANSP); Coffee Bay, Transkei (V. Orr, 1955; ANSP); Port Alfred (USNM); (AWBP coll.); near Durban (Mrs. N. Prior).

Patella depsta Reeve, 1855

(Pl. 77, pl. 78, fig. 1)

Range—Islands of St. Paul and Amsterdam, South Indian Ocean.

Remarks—Reeve cited "Macao and the Island of St. Paul" as localities for this species, but the first mentioned location is obviously a mistake. St. Paul is here nominated as the type locality. The species also occurs at the adjacent island of Amsterdam.

Gaillard (1954) figured the radula of *depsta*, and assigned the species to *Cellana*, but the radula suggests much closer alliance with the Patellinae, and except for the laterals, is not unlike that of *Patella* (*Patellona*). The laterals in the Patellinae are usually fused at the base, and have a pluricuspid head, but Gaillard's drawing shows a pair of laterals on either side, each separated at the base. Since the writer has no preserved material of this species the

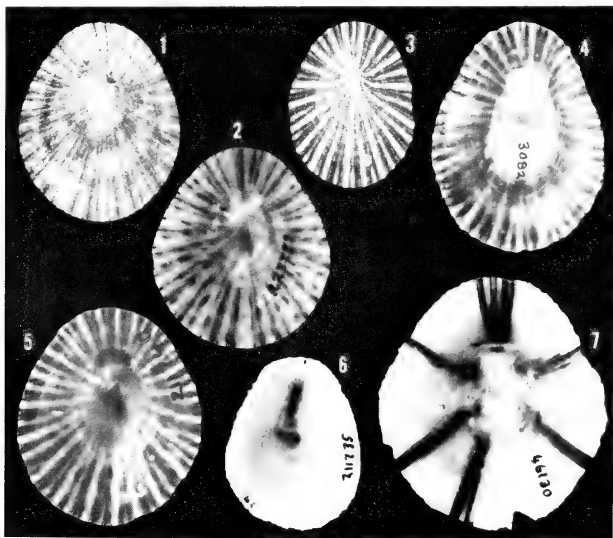


Plate 76. Figs. 1-7. *Patella concolor* Krauss, 1848. Figs. 1, 2. Port Alfred, South Africa, 35-36 mm., AWBP coll. 30872; 227788. Figs. 3, 4. Port St. John's, Pondoland, South Africa, 26-34 mm., AWBP coll. 30822. Fig. 5. Coffee Bay, Transkei,

South Africa, 30 mm., AWBP coll. 48225. Fig. 6. Umtwalumi, South Africa, 34 mm., AWBP coll. 211735. Fig. 7. South Africa, 50 mm., AWBP coll. 46130.



Plate 77. *Patella depsta* Reeve, 1854. Island of St. Paul, South Indian Ocean, 32-35 mm., AWPB coll. 46133.

apparently unusual form of the laterals cannot be confirmed at present.

Description—Shell of moderate size, up to 35.5 mm. (1½ inches) in length, lightly built, ovate, gradually narrowed in front, and moderately elevated, with the apex anterior to the middle, compressed and hooked. Sculptured finely and delicately radially lirate, arranged more or less in fours, the inner two weaker than the outer two, and about 100 lirae in all. Colour of exterior pale pinkish chestnut; interior orange-brown with a slight bronzy sheen; spatula pinkish white.

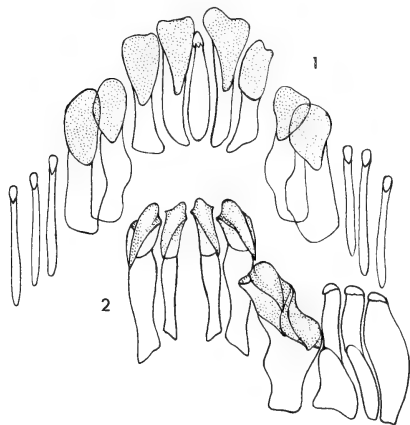


Plate 78. Fig. 1. *Patella depsta* Reeve, Island of St. Paul. Radula, from Gaillard, 1954, p. 521, fig. 1. Fig. 2. *Patella concolor* Krauss, Natal. Radula, from Koch, 1949, p. 511, fig. 22 (as *variabilis* Krauss).

Measurements (mm.)—(both A. W. B. Powell collection).

length	width	height
35.5	28.0	14.0
32.25	24.0	12.0
		St. Paul
		St. Paul

Radula—Formula $3 + 2^2 + (2+1+2) + 2^2 + 3$.

Synonymy—

- 1855 *Patella depsta* Reeve, Conch. Iconica, pl. 31, figs. 85 a, b. (Jan.).
 1891 *Helcioniscus depsta* Reeve, Pilsbry, Man. Conch., vol. 13, p. 151, pl. 20, figs. 45, 46.
 1954 *Cellana depsta* Reeve, Gaillard, Bull. Mus. Nat. d'Hist. Nat., vol. 26, pp. 520, 521, text. fig. 1 (radula).

Patella rangiana Rochebrune, 1882

(Pl. 75, figs. 5, 6)

Range—Porto Praya, Cape Verde Islands.

Remarks—This species, which the writer has not seen, appears to be a distinctive one, with its very scaly prominent radial ribs. Pilsbry's translation of the original description follows, accompanied by copies of Rochebrune's figures.

Description—"Shell ovate, depressed-convex, rufous; vertex submucronate, usually eroded, situated at 2/3 of the length; having larger and smaller radiating broad, very scaly ribs, scales subimbricating, obtuse, lenticular; margin undulating; interior bluish, silvery-pearly, rayed with bands and spots of purplish, the center spatulate."

Measurements (mm.)—

length	width	height
44.0	36.0	19.0
		(Rochebrune)

Synonymy—

- 1882 *Patella rangiana* Rochebrune, Bull. Soc. Philomathique, Paris, ser. 7, vol. 6, p. 29.
 1891 *Patella rangiana* Rochebrune, Pilsbry, Man. of Conch., vol. 13, p. 89, pl. 58, figs. 42, 43.

? *Patella kaffraria* Rennie, 1930

(Pl. 79)

Range—Upper Cretaceous of Pondoland, South Africa.

Remarks—The author of this species remarked that "It need hardly be stated that the genus *Patella* is here used in the widest possible sense. The species is apparently distinct from any previously described from the Cretaceous." It certainly appears to belong to the Patellacea, but a precise generic or even familial allocation would be purely conjectural. Rennie's original description follows.



Plate 79. *Patella kaffraria* Rennie, 1930. Upper Cretaceous of Pondoland, South Africa, 32.5 mm. Holotype, from Rennie, 1930, pl. 24, figs. 1, 2.

Description—"Shell moderately convex, with the apex obtusely pointed, not recurved, and placed well in front of the middle; the sides are straight, or only slightly convex. Aperture oval,

considerably longer than wide, with wavy margin. Surface with stout, rather irregular, radial ribs, and narrow furrows; on the posterior side the ribs are of two sizes, the larger and smaller alternating; on the anterior side there are more numerous, finer ribs; the ribs are crossed by irregular growth markings."

Measurements (mm.) (Not stated, but evidently the figures are natural size)—

length	width	height	
32.5	25.0	14.0	holotype

Synonymy—

1930 *Patella kaffraria* Rennie, *Annals of South African Museum*, vol. 28, p. 206, pl. 24, figs. 1-4.

Types—The holotype (No. 8477) and paratype (No. 8572) are in the South African Museum.

Patella granatina Linnaeus, 1758

(Pl. 64, figs. 1-3; pl. 80; pl. 82, fig. 2)

Subgenus Patellona Thiele in Troschel, 1891Type: *Patella granatina* Linnaeus, 1758

This group of patellids was named because of a marked difference in the radula from that of typical *Patella*. The four central teeth of true *Patella* occur in a horizontal alignment whereas in *Patellona* there is a median central, narrower and of smaller size than the outer pairs of centrals, which instead of being in line, descend steeply to the laterals, their tops forming a chevron. The cusps of the centrals and laterals vary between oblique heart-shape and parrot-beaklike.

This chevron-like radula is found in species from Cape Verde Islands, Senegal, Guinea, Angola and St. Helena, as well as South Africa, where the type species *granatina* and the related *oculus* occur, these two being more or less restricted to the cooler waters of the west coast. Shells of this subgenus are slightly iridescent within and the shell substance is sufficiently transparent for the external colour patterns to show through faintly.

The northward flowing cool Benguela Current could account for the presence of the subgenus in Angola and St. Helena, but locations north of there, in the tropical waters of West Africa and the Cape Verde Islands, are, under present conditions, out of range of the influence of that current. Nevertheless the style of radula in the tropical West African and Cape Verde Islands limpets is so similar to that of the cool water species of the South African west coast that some distributional continuity, under more uniform hydrological conditions, must have existed in the past.

Related to *Patellona* is the subgenus *Cymbula* (see ahead) in which the central teeth have the same chevronlike alignment, but their cusps are distinctive in having broad blunt tops with raised marginal rims.

Synonymy—

1891 *Patellona* Thiele in Troschel, Das Gebiss der Schnecken, vol. 2, p. 317, for *granatina* Linnaeus, 1758, *adansonii* Dunker, 1853 and *plumbea* Lamarck, 1819. Type, by subsequent designation, Tomlin, 1931: *Patella granatina* Linnaeus, 1758.

Range—South Africa, Port Nolloth on the west coast, south to False Bay and extending eastward to Danger Point.

Remarks—This large but relatively thin South African limpet is easily recognised by its broadly ovate, almost pentagonal outline, strong, narrowly crested, radial ribs, and distinctive coloration of the interior which is bluish white with a clearly outlined dark-brown spatula.

Description—Shell large, up to 85 mm. (3½ inches) in length, strong but of relatively light build, broadly ovate and tall-conical, with the apex almost central. Sculpture of radiate folds that strongly corrugate the margin; five of the radials on the posterior half of the shell are stronger than the rest; radials and interspace alike bear closely-spaced cords that are rendered scabrous by dense concentric growth-lamellae. Colour of exterior greyish to dull-white with an underlying pattern of dark-brown, zigzag, concentric markings, often forming a netted design; interior bluish white, the spatula dark-chocolate, with clearly defined edges, and a marginal pattern of numerous short, dark-brown dashes, with regular gaps corresponding to the external primary radials.

Radula—Formula $3 + 1 + (2 + 1 + 2) + 1 + 3$. The median central is small and slender, flanked by a pair of stout fully-developed centrals on either side, followed by a pluricuspid lateral, and the usual three, more or less functionless, marginals. The centrals, collectively, form a chevron, as in other members of this subgenus. The cusps of the paired centrals and the pluricuspid laterals are leaf-shaped, obliquely flexed, and with a median groove or depression.

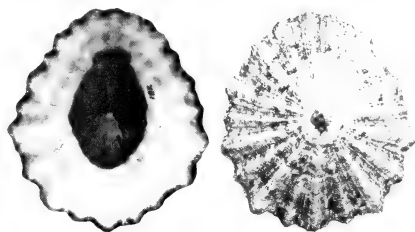


Plate 80. *Patella (Patellona) granatina* Linnaeus, 1758. Table Bay, South Africa, 71 mm., AWBP coll. 183.

Measurements (mm.)—(all A. W. B. Powell collection)

length	width	height	
85.0	78.5	30.0	South Africa
74.0	63.5	35.0	South Africa
60.0	49.5	20.0	False Bay

Synonymy—

- 1758 *Patella granatina* Linnaeus, Syst. Nat. ed. 10, p. 782.
 1819 *Patella apicina* Lamarck, Anim. sans vert., vol. 6 (1), p. 324.
 1848 *Patella granatina* Lam., Krauss, Sudafr. Moll., Stuttgart, p. 43.
 1854 *Patella granatina* Lam., Reeve, Conch. Iconica, pl. 3, figs. 4 a, b.
 1891 *Patella (Scutellastra) granatina* Lam., Pilsbry, Man. Conch., vol. 13, p. 106, pl. 62, figs. 76, 77.
 1891 *Patellona granatina* Lam., Thiele, Das Gebiss der Schnecken, vol. 2, p. 317.
 1931 *Patellona granatina* Lam., Tomlin, Ann. Natal Mus., vol. 6 (3), p. 417 (designated type of *Patellona*)
 1949 *Patella granatina* Lam., Koch, Ann. Natal Mus., vol. 11 (3), p. 501, pl. 20, figs. 1-5; text figs. 9, 10 (radula)

Records—SOUTH AFRICA: Table Bay (AWBP coll.); False Bay (AWBP coll.); Platboom, Cape Peninsula (V. Orr, 1955; ANSP); Sea Point (Mrs. N. Prior) Simonstown (AWBP coll.).

***Patella oculus* Born, 1778**

(Pl. 64, figs. 7-9; pl. 81; pl. 82, fig. 1)

Range—South Africa, west coast from near Cape Town eastward to Umhlangi.

Remarks—This large, depressed, broadly-ovate,

star-shaped limpet has something of the appearance of *Patella (Scutellastra) longicosta* Lamarck, but differs from it, not only in dentition, but also in coloration, for the interior of *oculus* is dark purplish brown, except for a yellowish brown spatula and a surrounding area of light bluish grey. The species is essentially a cold-water one, and is more abundant along the west coast of South Africa than to the eastward. It occurs in the Balaenoid zone, which is lower mid-tidal, but sometimes extends to and below low spring-tide level.

Description—Shell large, up to 110 mm. (4½ inches) in length, solid, depressed, broadly ovate, star-shaped, with the principal ribs strongly corrugating the margin. Sculpture consisting of about 11 primary, broad, carinated radials, plus secondary radials and interstitial threads. Colour of exterior dull-brown to blackish, but usually eroded to dull-light greyish brown; interior with a very broad dark purplish brown border, and a light bluish grey area surrounding the spatula, which is fawn to deep yellowish brown.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3, very similar to the radula of *granatina*, the central teeth having the same chevronlike alignment.

Measurements (mm.)—

length	width	height	
110.0	106.0	42.0	Cape of Good Hope
86.0	76.0	15.0	Port Elizabeth
73.0	63.0	15.0	Port Alfred
53.0	51.0	8.0	Still Bay

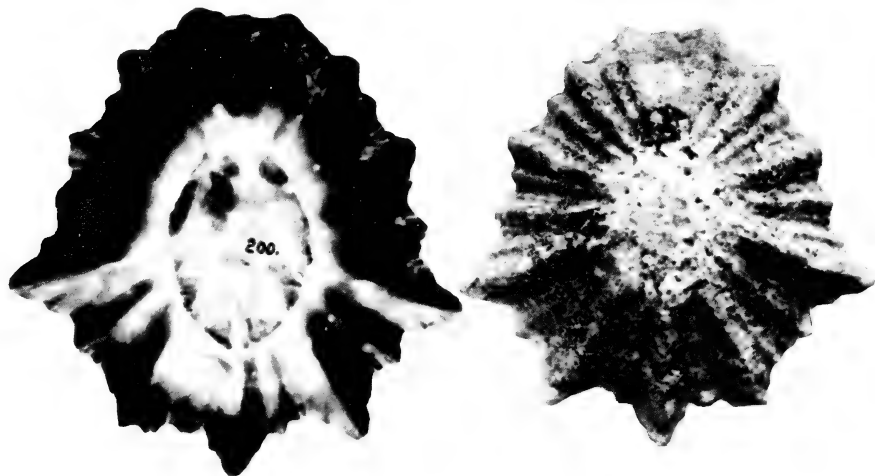


Plate 81. *Patella (Patellona) oculus* Born, 1778. Cape of Good

Hope, South Africa, 77 mm., AWBP coll. 200.

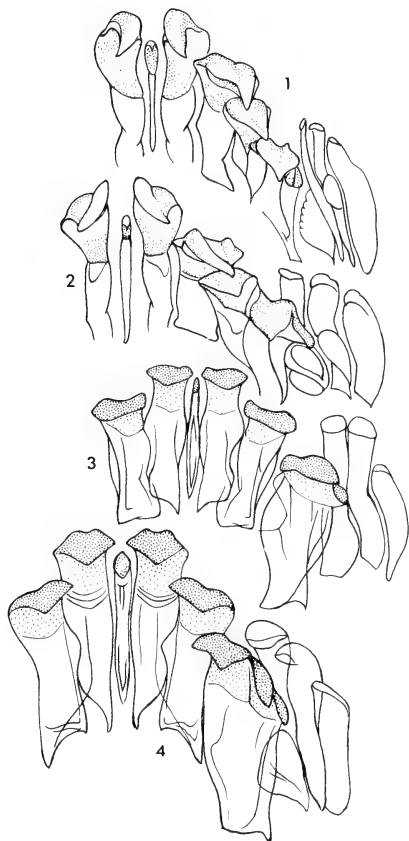


Plate 82. Fig. 1. *Patella (Patellona) oculus* Born, South Africa. Radula, from Koch, 1949, p. 508, fig. 18. Fig. 2 *Patella (Patellona) granatina* Linnaeus, South Africa. Radula, from Koch, 1949, p. 502, fig. 10. Fig. 3. *Patella (Patellona) canescens* Gmelin, St. Helena. Radula, from Thiele, 1891, pl. 28, fig. 7 (as *plumbea* Lamarck). Fig. 4. *Patella (Patellona) adansonii* Dunker, "Chinchao" in error, probably West Africa. Radula, from Thiele, 1891, pl. 28, fig. 8.

Synonymy—

- 1778 *Patella oculus* Born, Index Mus. Caes. Vind., p. 434.
 1786 *Patella oculus hirci* Lightfoot, Cat. Portland Mus., p. 105.
 1791 *Patella badia* Gmelin, Syst. Nat., ed. 13, p. 3700.
 1791 *Patella monopis* Gmelin, Syst. Nat., ed. 13, p. 3707.
 1791 *Patella fuscescens* Gmelin, Syst. Nat., ed. 13, p. 3701.
 1798 *Patella astrolepas* Röding, Mus. Bolten., vol. 2, p. 12.
 1819 *Patella scutellaris* Lamarck, Anim. sans vert., vol. 6 (1), p. 328.

- 1848 *Patella schroeteri* Krauss, Südafr. Moll., Stuttgart, p. 43.
 1854 *Patella oculus* Born, Reeve, Conch. Iconica, pl. 2, figs. 2 a, b.
 1891 *Patella (Scutellastra) oculus* Born, Pilsbry, Man. Conch., vol. 13, p. 106, pl. 27, figs. 30-32.
 1932 *Patella oculus* Born, Turton, Mar. Shells Port Alfred, p. 162.
 1932 *Patella oculus badia* Gmelin, Turton, Mar. Shells Port Alfred, p. 163.
 1932 *Patella oculus fuscescens* Gmelin, Turton, Mar. Shells Port Alfred, p. 163.
 1932 *Patella oculus schroeteri* Krauss, Turton, Mar. Shells Port Alfred, p. 163.
 1932 *Patella oculus planulata* Turton, Mar. Shells Port Alfred, p. 163.
 1942 *Patella oculus* Born, Tomlin & Stephenson, Proc. Malac. Soc., Lond., vol. 25, pp. 5, 6.
 1949 *Patella oculus* Born, Koch, Ann. Natal Mus., vol. 11 (3), p. 507, pl. 22, figs. 1-4; text figs. 17, 18 (radula).
 1967 *Patella scutellaris* Lamarck, Christiaens, Bull. Mus. Nat. d'Hist. Nat. ser. 2, vol. 39 (5), p. 973.

Records—SOUTH AFRICA: west coast near Cape Town, eastward to Umhlabi (Koch, 1949, p. 507); Cape of Good Hope (AWBP coll.); False Bay (AWBP coll.); Buffel's Bay, Cape Peninsula (Mrs. N. Prior); Still Bay (Auck. Mus.); Port Elizabeth (Auck. Mus.); Jeffrey's Bay (Auck. Mus.); Port Alfred (AWBP coll.).

Patella adansonii Dunker, 1853

(Pl. 82, fig. 4; Pl. 83, figs. 5, 6)

Range—West Africa.

Remarks—This species is characterised by its dense fine radial ribbing, brown-lined and marbled external pattern, and finely denticulated margin.

Description—Shell of moderate size, 36-50 mm. (1½-2 inches) in length, ovate, the anterior end slightly narrowed, moderately elevated, with the apex at about the anterior third. Sculpture consisting of about 80 to 100 narrowly-rounded radial ribs that more or less alternate in strength. Colour, externally whitish, marbled, and radially and narrowly streaked with olive or dark greenish brown, internally pale bluish grey, with the external pattern showing through, more strongly at the margin; spatula buff to pale orange-brown.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. The five central teeth are not in a straight horizontal row as in typical *Patella*, for the outer pair of centrals are lower than the inner pair, and the median one is small, very slender and almost vestigial.

Measurements (mm.)—

length	width	height	
50.0	41.0	17.0	Pilsbry, 1891, p. 92
42.0	33.0	14.0	Angola

Synonymy—

- 1853 *Patella adansonii* Dunker, Ind. Moll. Guin. Infer., p. 42, pl. 6, figs. 10-15.
 1891 *Patella adansonii* Dunker, Pilsbry, Man. Conch., vol. 13, p. 92, pl. 12, figs. 30-33.

Records—WEST AFRICA: Loanda (type); Ambrizette, Angola (AWBP coll.; ANSP).

***Patella canescens* Gmelin, 1791**

(Pl. 82, fig. 3; Pl. 83, figs. 3, 4)

Range—St. Helena.

Remarks—The sculpture is much finer than that in either *lugubris* or *plumbea* and in consequence the shell margin is delicately crenulated rather than corrugated.

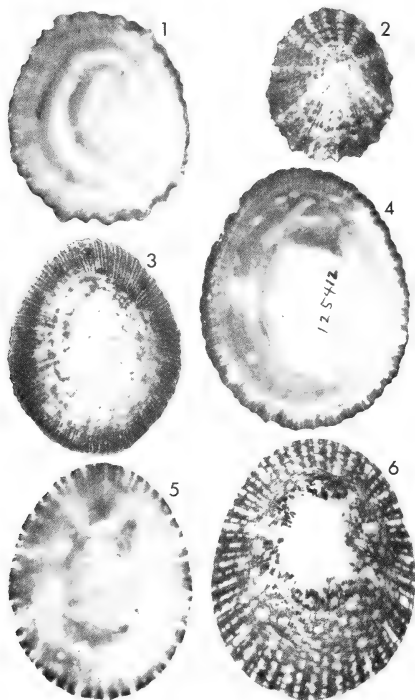


Plate 83, Figs. 1, 2. *Patella (Patellona) lugubris* Gmelin, 1791. Porto Grande, St. Vincent, Cape Verde Islands, 42-54 mm., AWBP coll. 50089. Figs. 3, 4. *Patella (Patellona) canescens* Gmelin, 1791. St. Helena, 41-45 mm., AWBP coll. 125412. Figs. 5, 6. *Patella (Patellona) adansonii* Dunker, 1853, Angola, West Africa, 36-42 mm., AWBP coll. 146139.

Description—Shell of moderate size, up to 47 mm. (1½ inches) in length, ovate, slightly narrowed in front, moderately elevated, with the apex subcentral. Sculpture crisp, consisting of very numerous radial cords, the primaries grouped in pairs or in threes, with an occasional intermediate between each group of primaries. Colour of exterior black, usually eroded to a greyish brown. Interior bluish silvery, the spatula flesh to orange-brown, and the edge of the shell narrowly margined in black.

Measurements (mm.)—

length	width	height	
47.0	40.0	20.0	St. Helena; Christiaens, 1968
45.0	37.5	20.0	St. Helena

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Radula very similar to that of *plumbea* and *adansonii*, with the median central very small and the pairs of centrals arranged chevron-like, descending sharply from the central line. The lateral is distinctive in having four well developed cusps (Christiaens, 1968, text fig. 1).

Synonymy—

- 1791 *Patella canescens* Gmelin, Syst. Nat., ed. 13, p. 3724. Locality?
 1855 *Patella canescens* Gmelin, Reeve, Conch. Iconica, pl. 34, figs. 103 a, b. Locality?
 1968 *Patella canescens* Gmelin, Christiaens, Rev. Zool. Bot. Afr., vol. 77, pts. 3-4, pp. 314-320. St. Helena.

***Patella lugubris* Gmelin, 1791**

(Pl. 83, figs. 1, 2)

Range—West Africa, Loanda, Benguela, Guinea and Cape Verde Islands.

Remarks—The species is much more coarsely ribbed than either the St. Helena *canescens* or the West African *plumbea*, and from the latter species it differs in being more broadly ovate.

Description—Shell moderately large, up to 60 mm. (2½ inches) in length, broadly ovate, moderately elevated, with the apex almost at the anterior third. Sculpture consisting of numerous strong, keeled radials that prominently corrugate the margin. Colour, externally dull-black, internally silvery bluish grey, the spatula often clouded with a white callus.

Measurements (mm.)—

length	width	height	
60.0	50.0	20.0	Pilsbry, 1891, p. 91
53.0	46.0	19.0	Cape Verde Islands

Synonymy—

- 1791 *Patella lugubris* Gmelin, Syst. Nat. ed. 13, p. 3705; based upon Martini-Chemnitz, Conch. Cab., vol. 1, pl. 8, fig. 60.
 1854 *Patella lugubris* Gmelin, Reeve, Conch. Iconica, pl. 14, figs. 32 a-c. "Island of St. Vincent, West Indies," sic. — St. Vincent, Cape Verde Islands.
 1891 *Patella lugubris* Gmelin, Pilsbry, Man. Conch., vol. 13, p. 90, pl. 12, figs. 39, 40, 41-44; pl. 57, figs. 32-35.

Patella plumbea Lamarck, 1819

(Pl. 84)

Range—Senegal, West Africa.

Remarks—This species is closely allied to *lugubris*, and when adequate material is studied, may prove to be identical. Pilsbry (*l. c.*) remarked that "the ribbing is finer than in *P. lugubris*, the shell is more elliptical, more depressed, and the central spatula of the interior is longer and narrower."

Description—Shell moderately large, up to 53 mm. (2-1/16 inches) in length, narrowly ovate, low-conical. Colour, externally dull-black, internally bluish, the spatula whitish, often clouded with brown.

Measurements (mm.)—

length	width	height
52.0	38.0	10.5

type; Mermod, 1950, p. 692

Synonymy—

- 1819 *Patella plumbea* Lamarck, Anim. s. Vert., vol. 6, p. 328.
 1834 *Patella caerulea* Quoy and Gaimard, Voy. Astrolabe, Moll., vol. 3, p. 342, pl. 70, figs. 4-6.
 1854 *Patella plumbea* Lam., Reeve, Conch. Iconica, pl. 3, figs. 5 a, b.

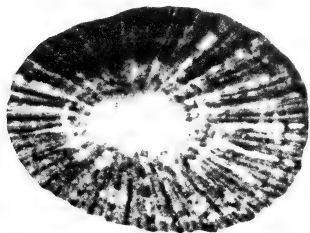


Plate 84. *Patella (Patellona) plumbea* Lamarck, 1819. Senegal, West Africa. Holotype, 52 mm., from Mermod, Rev. Suisse Zool., vol. 57, no. 34, p. 693, fig. 4.

- 1891 *Patella plumbea* Lam., Pilsbry, Man. Conch., vol. 13, p. 91, pl. 24, figs. 11, 14, 15; pl. 57, figs. 38, 39.
 1950 *Patella plumbea* Lam., Mermod, Rev. Suisse Zool., vol. 57, no. 34, pp. 692, 693, text fig. 4 (type).

Patella safiana Lamarck, 1819

(Pl. 72, figs. 3, 4)

Range—Algeria, Morocco and West Africa.

Remarks—This is a large, elongate-ovate species, only moderately elevated, and with a long narrow spatula. In coloration the exterior is whitish, with conspicuous brown rays in the rib interstices. The interior is silvery grey, with the brown external rays showing through towards the margin; the spatula is creamy-white, often stained with orange-brown.

Description—Shell large, up to 77 mm. (3 inches) in length, elongate-ovate, moderately elevated, with the apex at about the anterior third. Sculptured with broadly rounded primary radial ribs and weak interstitial cords. Colour: externally with whitish primary ribs and the interstices intermittently rayed with brown; internally buff to silvery-grey, slightly iridescent; spatula cream, clouded with light orange-brown.

Radula—Formula 3 + 1 + 4 + 1 + 3. The radula resembles that of *adansonii*, *canescens* and *plumbea*, in that the centrals are not in a horizontal line, the outer pair being lower than the inner pair. Also, a median central appears to be completely absent, as in *vulgata* (see Fischer-Piette, 1935, p. 53, text fig. 22).

Measurements (mm.)—

length	width	height
77.0	57.0	21.0
65.0	51.0	21.0

largest of Lamarck's type series
Oran, Algeria**Synonymy—**

- 1819 *Patella safiana* Lamarck, Anim. sans vert., vol. 6, p. 329.
 1849 *Patella conspicua* Philippi, Abbild., vol. 3, p. 71. Guinea.
 1852 *Patella kraussii* Dunker, Index Moll. Guin. inf., p. 42, pl. 6, figs. 4-6.
 1854 *Patella conspicua* Philippi, Reeve, Conch. Iconica, pl. 7, fig. 12. Gaboon.
 1891 *Patella safiana* Lam. Pilsbry, Man. Conch., vol. 13, p. 90, pl. 55, figs. 19-21.
 1935 *Patella safiana* Lam. Fischer-Piette, Journ. Conchyl., vol. 79, p. 53.
 1950 *Patella safiana* Lam., Mermod, Rev. Suisse Zool., vol. 57, no. 34, pp. 693, 694, text fig. 5.

Types—The type series of *safiana* is in the Muséum D'Histoire Naturelle de Genève.

Records—ALGERIA: Oran (AWBP coll.). MOROCCO: ocean coast (Pilsbry, 1891). WEST AFRICA: Gaboon, Guinea (Philippi, 1849, type of *conspicua*).

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus *Patellidea* Thiele in Troschel, 1891

Type: *Patella granularis* Linnaeus, 1758

This subgenus, of which the type species is the only known member, appears to be most closely allied to the subgenus *Scutellastra*. The radula resembles that of *Scutellastra* in its main features, especially in having a narrow but well-developed median central, and the other 4 larger centrals in a horizontal line, but differs in the form of the cusps which are oblique and parrot-beaklike.

The shell also differs from that of *Scutellastra* in texture in being more strongly coloured, and in having distinctive external sculpture, consisting of strong radials bearing prominent imbricated scales. Recent, South Africa.

Synonymy—

1891 *Patellidea* Thiele in Troschel, Das Gebiss der Schnecken, volume 2, p. 315. Type, by monotypy: *Patella granularis* Linnaeus, 1758.

Patella granularis Linnaeus, 1758

(pl. 64, figs. 4-6; pls. 85-87)

Range—South Africa, the entire coastline from Port Nolloth in the west to Umpangazi in the east.

Remarks—This common South African species is easily identified by its scaly external ribbing and bluish white interior, broadly margined in dark-

brown, and with a reddish brown spatula.

Reeve's *Patella vidua*, erroneously recorded from the Philippines, is a synonym. A photograph of one of Reeve's figured specimens (Fig. 22a) was kindly supplied by Dr. J. D. Taylor, and that specimen, in the collections of the British Museum (Natural History), is here nominated lectotype of *vidua*.

Description—Shell of moderate size, up to 63 mm. (2½ inches) in length, ovate, slightly narrowed in front, tall-conical, with the apex slightly anterior of the centre. Sculpture of strong, regular, rounded primary radial ribs, with slightly weaker intermediates; 1 to 3 intermediates between the primary radials; all ribs with closely-spaced, imbricated, scales, resultant from numerous, lamellose concentric growth lines. Colour: externally dull light-brown to grey, with the scales paler; internally bluish white, with a dark-brown, wide, marginal border, and a reddish brown spatula. In fully grown examples the border is usually continuous, but in young shells it is interrupted by bluish white radial streaks, corresponding with the external radials.

Radula—Formula $3 + 1 + (2+1+2) + 1 + 3$. Central teeth 5, the middle member small and slender, almost vestigial, the outer pairs much larger, each with a long, pointed and incurved cusp; pluricuspid lateral with an enlarged top, bearing 4 cusps, of which the second from the proximal side is largest, and shaped like those of the central pairs; marginals 3, long, narrow and flexuous, each with a rudimentary cusp.

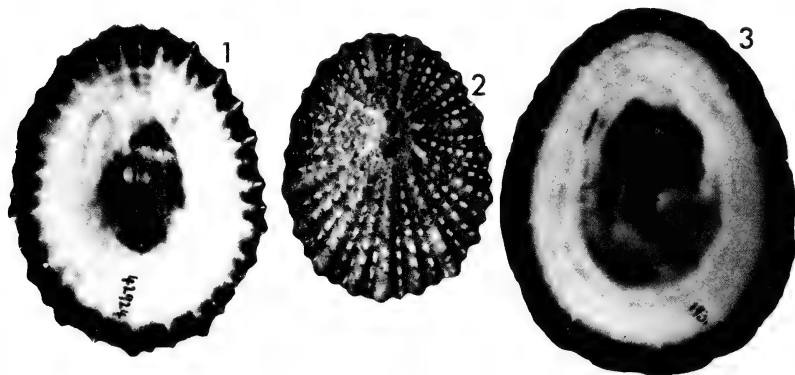


Plate 85. *Patella (Patellidea) granularis* Linnaeus, 1758. Figs. 1, 2. Platboom, Cape Point, South Africa. Fig. 3. Cape of

Good Hope, South Africa, 37-60 mm., AWBP coll. 42924 & 193.

Measurements (mm.)—

length	width	height	
63.0	48.0	19.0	Sea Point; Mrs. N. Prior
59.0	49.0	26.0	C. of Good Hope
49.0	38.0	24.0	Platboom
44.5	36.0	17.0	Port Alfred

Synonymy—

- 1758 *Patella granularis* Linnaeus, Syst. Nat., ed. 10, p. 782.
 1834 *Patella granularis* L., Quoy and Gaimard, Voy. 'Astrolabe', Zool. vol. 3, p. 341, pl. 70, figs. 12-15.
 1848 *Patella granularis* L., Krauss, Sudafr. Moll., Stuttgart, p. 52.
 1848 *Patella echinulata* Krauss, Sudafr. Moll., Stuttgart, p. 52, pl. 3, fig. 15.
 1848 *Patella natalensis* Krauss, Sudafr. Moll., Stuttgart, p. 53, pl. 3, fig. 10.
 1854 *Patella vidua* Reeve, Conch. Iconica, pl. 11, figs. 22a, b.
 1854 *Patella granularis* L., Reeve, Conch. Iconica, pl. 14, figs. 31a, b.
 1855 *Patella morbida* Reeve, Conch. Iconica, pl. 25, figs. 64a, b.
 1891 *Patella (Scutellastra) granularis* L., Pilsbry, Man. Conch., vol. 13, p. 102, pl. 63, figs. 80-83.
 1891 *Patellidea granularis* L., Thiele (new genus), in Troschel & Thiele, Das Gebiss der Schnecken, col. 2, p. 315.
 1931 *Patellidea granularis* Linne', (designated type of genus) Tomlin, Ann. Natal Mus., vol. 6 (3), p. 417.
 1932 *Patella granularis* L., Turton, Mar. Shells Port Alfred, p. 166.

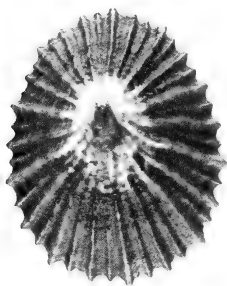


Plate 86. *Patella (Patellidea) granularis* Linnaeus, 1758. Lectotype, here nominated, of *Patella vidua* Reeve, 1854, erroneously recorded from the Philippines, but considered to be synonymous with the South African *granularis*. The lectotype is based upon Reeve's fig. 22a. Photo by courtesy of Dr. J. D. Taylor, British Museum (Natural History).

- 1932 *Patella morbida* Reeve, Turton, Mar. Shells Port Alfred, p. 166.
 1932 *Patella natalensis* Krauss, Turton, Mar. Shells Port Alfred, p. 166.
 1932 *Patella natalensis echinulata* Krauss, Turton, Mar. Shells Port Alfred, p. 166.
 1932 *Patella miliaris* Turton, Mar. Shells Port Alfred, p. 166. (non Philippi, 1848)
 1932 *Patella argenvillei assimilans* Turton, Mar. Shells Port Alfred, p. 167.
 1932 *Patella alboradiata* Turton, Mar. Shells Port Alfred, p. 167.
 1933 *Patella tomlini* Turton, (nom. nov. pro *P. alboradiata* Turton, 1932, non Gmelin, 1791) Journ. Conch., vol. 19, p. 371.
 1949 *Patella granularis* Linne', Koch, Ann. Natal Mus., vol. II (3), p. 503, pl. 19, figs. 4-8; text figs. 11, 12 (radula).

Types—The types of *granularis* (Holotype; Sloane coll., no. 1013), *morbida* and *vidua* (lectotype, here selected) are in the British Museum (Natural History).

Records—SOUTH AFRICA: Port Nolloth to Umpangazi, north of Durban (Koch, 1949, p. 503); Saldanha Bay (Discovery II, 1926); Table Bay (AWBP coll.); Cape of Good Hope (AWBP coll. 193); Sea Point (Mrs. N. Prior); False Bay (Auck. Mus.); Platboom, Cape Point (V. Orr, Jan. 1955); Jeffrey's Bay (AWBP coll.); Port Alfred (Auck. Mus.).

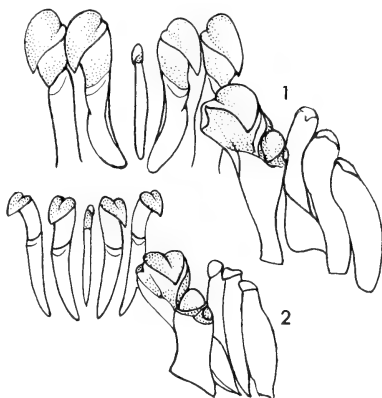


Plate 87. Fig. 1. *Patella (Patellidea) granularis* Linnaeus. South Africa. Radula. Fig. 2. *Patella (Olana) cochlear* Born. Radula, both from Koch, 1949, p. 504, fig. 12 & p. 499, fig. 6.

Subgenus *Cymbula* H. and A. Adams, 1854

Type (monotypy): *Patella compressa* Linnaeus, 1758

This subgenus contains two species, the shells of which are of very different outward appearance, but nevertheless have a striking sameness in the radula that is of a distinctive type. The multiple centrals and the pluricuspid lateral have large blunt-topped cusps, with strongly raised or flanged edges. The centrals collectively form a chevron instead of forming a horizontal line, as in typical *Patella*, and thus indicate alliance with the subgenus *Patellona*.

The type species is the easily recognised *compressa*, with its elongated, laterally compressed shell, adapted to its specialised station on the stipes of the large kelps, *Ecklonia* and *Laminaria*. Only rarely is this species found attached to rock. On the other hand, the second species, *miniata*, is of normal ovate limpet shape, since it is exclusively a rock-dweller. Both species are restricted to South African waters.

Synonymy—

- 1854 *Cymbula* H. Adams and A. Adams, The Genera of Recent Mollusca, volume 1, p. 466. Type, by monotypy: *Patella compressa* Linnaeus, 1758. [*Cymbula* Gray, 1821, is an error for *Cymbulia* Peron and Lesnèr 1810].

Patella compressa Linnaeus, 1758

(pl. 63, fig. 9; Pls. 88, 89)

Range—South Africa, from Port Nolloth in the west to Danger Point in the south. Records from further afield, including one from St. Helena, are due to drift, along with large algae, upon which the species lives.

Description—Shell large, up to 117.5 mm. (4½ inches) in length, thin, elongate-ovate, tall and narrow, with parallel sides, the apex a little forward of the middle, and curving anteriorly. Sculpture consisting of very numerous, rather unequal, linear-spaced riblets; margin very minutely crenulated, convex at the sides, and concave at the ends. Colour: externally dull brownish buff; internally light pinkish fawn, the central area irregularly clouded with whitish callus.

Radula—Formula $3 + 1 + (2+1+2) + 1 + 3$. Central teeth 5, forming a chevron, the median one

small and very narrow, bearing a simple small cusp, outer pairs of centrals massive, each with a broad flat-topped cusp, ridged on each side, the ridges more prominent on the outermost teeth; pluricuspid lateral with two cusps, each similar to those of the outer centrals; the three marginals are small, each with a single simple cusp, outermost marginal largest of the three.

Measurements (mm.)—

length	width	height	
117.5	51.0	50.0	Kommetje, Cape Peninsula; Mrs. N. Prior.
94.0	45.0	35.0	South Africa; Pilsbry, 1891, p. 93
83.0	44.0	36.5	South Africa
63.5	35.0	23.0	South Africa

Synonymy—

- 1758 *Patella compressa* Linnaeus, Syst. Nat. ed. 10, p. 783.
 1834 *Patella compressa* L., Quoy and Gaimard, Voy. 'Astrolabe', Zool., vol. 3, p. 338, pl. 70, figs. 1-3.
 1848 *Patella compressa* L., Krauss, Südafr. Moll., Stuttgart, p. 50.
 1854 *Patella compressa* L., Reeve, Conch. Iconica, pl. 7, figs. 13a, b.
 1854 *Patella (Cymbula) compressa* L., H. & A. Adams, Gen. Rec. Moll., vol. 1, p. 466.
 1891 *Patella compressa* L., Pilsbry, Man. Conch., vol. 13, p. 93, pl. 61, figs. 68-70.
 1949 *Patella compressa* Linneé, Koch, Ann. Natal Mus., vol. 11, p. 499, pl. 17, figs. 4-6; text figs. 7, 8 (radula).

Records—SOUTH AFRICA: Port Nolloth to Danger Point (Koch, 1949, p. 499); Cape Peninsula (AWBP coll. 26039); Kommetje, Cape Peninsula (Mrs. N. Prior).

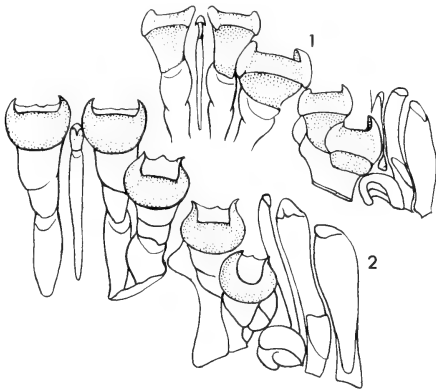


Plate 88. Fig. 1, *Patella (Cymbula) compressa* Linnaeus. South Africa. Radula, from Koch, 1949, p. 500, fig. 8. Fig. 2, *Patella (Cymbula) miniata* Born. South Africa. Radula, from Koch, 1949, p. 507, fig. 16.

***Patella miniata* Born, 1778**

(Pl. 63, figs. 10, 11; Pls. 88, 90, 91)

Range—South Africa, from Port Nolloth in the west, eastward to Qolora, near East London, and Natal.

Remarks—This moderately large, very attractive limpet is ovate, depressed and relatively thin, with an intricate pattern of radial streaks and speckles; it is reddish brown in living examples, but bleached to bright-pink in shells from beach drift. Pilsbry (1891, p. 93) was incorrect in assuming that *miniata* is merely a rock-dwelling ecotype of the kelp living *compressa*.

Description—Shell rather large, up to 93 mm. (3½ inches) in length, strong but relatively thin, ovate, slightly attenuated in front, rather depressed, and with the apex varying between sub-

central and the anterior third. Sculpture consisting of numerous primary radial cords, with mostly two radial threads in the interspaces; the ribbing varies in strength, and may be almost smooth to sharply-imbricated by dense concentric growth threads. Colour: externally radially streaked and speckled in reddish brown to bright-pink, on a white ground; internally silvery pinkish white, with the external pattern showing through strongly; spatula white-callused, sometimes tinged with orange. Living examples are usually encrusted.

Radula—Formula $3 + 1 + (2+1+2) + 1 + 3$. The radula stands nearest to that of *compressa*, the arrangement of the teeth being the same. The only noticeable difference between the two is in the shape of the cusps which have convex cutting edges in *miniata* but straight to concave ones in *compressa*.

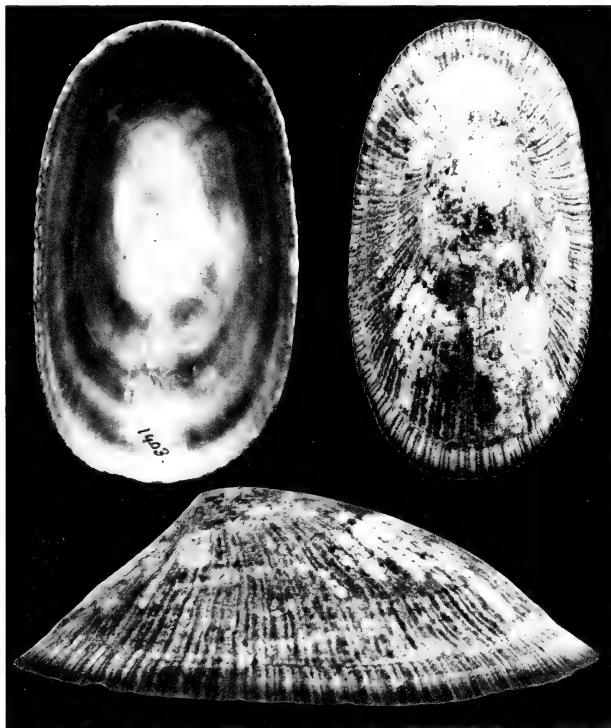


Plate 89. *Patella (Cymbula) compressa* Linnaeus, 1758. South Africa, 64-83 mm., AWBP coll. 1403 & 17985.

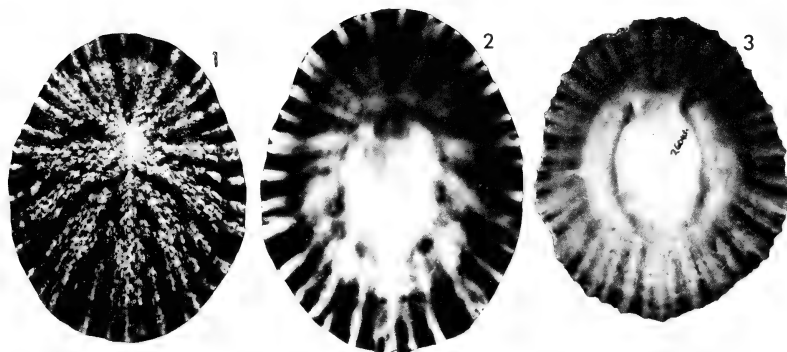


Plate 90. Figs. 1-3. *Patella (Cymbula) miniata* Born, 1778, South Africa. Figs. 1, 2. Port Nolloth, 75 mm., AWBP coll.

52455. Fig. 3. False Bay, 79 mm., AWBP coll. 26041.

Measurements (mm.)—

length	width	height	
93.0	71.5	22.0	Natal; Mrs. N. Prior.
79.0	66.0	20.0	False Bay
75.0	56.5	16.0	Port Nolloth
54.0	43.5	12.0	Still Bay

Synonymy

- 1778 *Patella miniata* Born, Index Mus. Caes. Vind., p. 436; 1780, Test. Mus. Caes. Vind., p. 420.
 1786 *Patella pulchra* Lightfoot, Cat. Portland Mus., p. 105.
 1791 *Patella umbella* Gmelin, Syst. Nat., ed. 13, p. 3706.
 1791 *Patella sanguinolenta* Gmelin, Syst. Nat., ed. 13, p. 3716.
 1798 *Patella rosea* Röding, Mus. Bolten., vol. 2, p. 9.
 1798 *Patella rubicunda* Röding, Mus. Bolten., vol. 2, p. 9.
 1848 *Patella miniata* Born, Krauss, Sudafr. Moll., Stuttgart, p. 51.
 1854 *Patella sanguinans* Reeve, Conch. Iconica, pl. 6, fig. 10.
 1854 *Patella umbella* Gmelin, Reeve, Conch. Iconica, pl. 9, figs. 17a, b.
 1891 *Patella compressa* var. *miniata* Born, Pilsbry, Man. Conch., vol. 13, p. 94, pl. 26, figs. 22-27.
 1932 *Patella miniata* Born, Turton, Mar. Shells Port Alfred, p. 168.
 1932 *Patella miniata umbella* Gmelin, Turton, Mar. Shells Port Alfred, p. 168.
 1932 *Patella miniata decorata* Turton, Mar. Shells Port Alfred, p. 169, pl. 39, fig. 1199.
 1932 *Patella pulchella* Turton, Mar. Shells Port Alfred, p. 169, pl. 39, fig. 1200. (non Blainville, 1825).
 1932 *Patella alboguttata* Turton, Mar. Shells Port Alfred, p. 169, pl. 39, fig. 1202.
 1932 *Patella denseplicata* Turton, Mar. Shells Port Alfred, p. 169, pl. 39, fig. 1205.
 1932 *Patella densestriata* Turton, Mar. Shells Port Alfred, p. 170, pl. 39, fig. 1206.
 1933 *Patella becki* Turton, Journ. Conch., vol. 19, p. 371; nom. nov. pro *P. pulchella* Turton, 1932, non Blainville, 1825.

1942 *Patella sanguinolenta* (sic Gmelin, Tomlin & Stephenson, Proc. Malac. Soc., Lond., vol. 25, p. 7.

1949 *Patella miniata* Born, Koch, Ann. Natal Mus., vol. 11 (3), p. 506, pl. 21, figs. 1-12; text figs. 15a, b, 16 (radula).

Records—SOUTH AFRICA: Port Nolloth in the west to Qolora in the east, common in the sub-littoral fringe (Koch, 1949, p. 506); Port Nolloth; False Bay; Still Bay; Port Elizabeth; Algoa Bay (all AWBP coll.); Natal (Mrs. N. Prior).

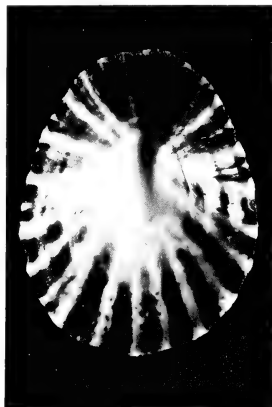


Plate 91. *Patella (Cymbula) miniata* Born, 1778. Natal, South Africa: An extra large and fine example of the species, in the collection of Mrs. Nancy Prior of Cape Town. It has a length of 93 mm. (3½ inches).

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Patella cochlear Born, 1778

(Pl. 63, figs. 12-14; Pls. 87, 92)

Range—South Africa, from Buffalo River on the west coast and around the Cape of Good Hope to Port Edward, Natal.

Description—Shell of moderately large size, up to 67 mm. (2½ inches) in length, solid, depressed, pear-shaped, with the anterior end much constricted, and produced like a spout. Sculptured with strong, rather unequal radial ridges that deeply corrugate the margin. Colour: externally white to yellowish brown; internally white, tinged with bluish grey; the spatula fawn, orange-brown, or clouded with white, and surrounded, except in front of the head region, with a broad band of indigo.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. The small, slender, median central tooth, and the two pairs of multiple centrals form a horizontal line, as in true *Patella*, but the massive lateral has four cusps, two of them large and the other two much smaller. The cusps are heart-shaped, with a pronounced groove down the middle; marginals 3, each with a weak cusp.

Measurements (mm.)—(all A. W. B. Powell collection).

length	width	height	
67.0	50.0	17.0	Port Alfred
58.5	43.5	15.5	Cape Natal
45.0	34.5	6.0	False Bay

Subgenus Olana H. and A. Adams, 1854

Type (monotypy): *Patella cochlear* Born, 1778

A moderate-sized shell of depressed pear-shape, with the anterior end laterally constricted and produced like a spout. The sole species of this subgenus is restricted to South Africa where in many places it is so abundant that it forms a dense mosaic, termed the "Cochlea zone." A density of 1,300 examples to the square-yard has been recorded, and as many as 40 crowded on top of a single large shell. Almost all large examples bear several deeply excavated scars, resultant from superimposed individuals. These limpets do not appear to move around much, but merely rotate, so that the head can move in a circle and the radula crop the algal growth within its range (See Koch, 1949, pp. 498-499).

Synonymy—

1854 *Olana* H. and A. Adams, The Genera of Recent Mollusca, vol. 1, p. 466. Type by monotypy: *Patella cochlear* Gmelin, 1791 = Born, 1778.

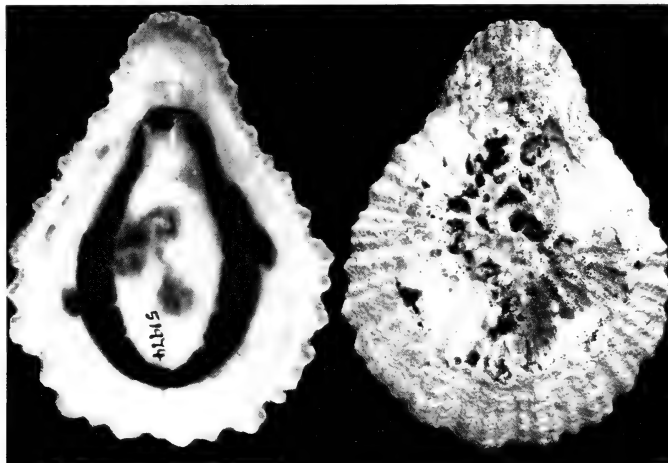


Plate 92. *Patella (Olana) cochlear* Born, 1778, Port Alfred,

South Africa, 66 mm., AWBP coll. 51974.

Synonymy—

- 1778 *Patella cochlear* Born, Index Mus. Caes. Vind., p. 437;
1780, Test. Mus. Caes. Vind., pl. 18, fig. 3, p. 420.
1790 *Patella cochlear* Born, Gmelin, Syst. Nat. ed. 13,
p. 3721.
1848 *Patella cochlear* Born, Krauss, Sudafr. Moll., Stuttgart,
p. 48.
1854 *Patella cochlear* Born, Reeve, Conch. Iconica, pl. 12,
figs. 24a, b.
1854 *Patella (Olana) cochlear* Born, H. & A. Adams, Gen.
Rec. Moll., vol. 1, p. 466.
1891 *Patella (Scutellastra) cochlear* Born, Pilsbry, Man.
Conch., vol. 13, p. 104, pl. 27, figs. 34, 35.
1949 *Patella cochlear* Born, Koch, Ann. Natal Mus., vol. 11
(3), p. 498, pl. 19, figs. 1-3; text figs. 5, 6 (radula).

Records—SOUTH AFRICA: False Bay; Sea Point (Mrs. N. Prior); Port Elizabeth; Cape Natal; Port Alfred (all AWBP coll.).

Subgenus *Scutellastra* H. and A. Adams, 1854

Type: *Patella barbara* Linnaeus, 1758

Mostly large massive shells with an opaque, non-iridescent, porcellaneous interior. The external coloration is either a uniform spread of colour, or the pigment may be confined to the spaces between the radial ribs and show through to the inside margin to form a narrow border where the shell is thinnest.

Radula and gill cordon as in typical *Patella*, but the median central tooth is usually well-developed, often as large as the other four centrals.

The range of the subgenus is South Africa, on across the Indo-Pacific as far east as the Society Islands, northward to Japan and along the south coast of Australia. Undoubted fossil occurrences of the subgenus are *cooperi* (Powell, 1938) from the lower Miocene of Motuihi Island, Auckland, New Zealand, and *aurorae* Fleming, 1973, from the middle Oligocene of Mason River, North Canterbury, New Zealand.

Synonymy—

- 1854 *Scutellastra* H. Adams and A. Adams, The Genera of Recent Mollusca, volume 1, p. 466, for *gorgonica* Humphrey, *pentagona* Born and *plicata* Born. Type, by subsequent designation. Powell, 1938: *Patella gorgonica* Humphrey "*=P. longicosta* Lamarck" (sic) *=Patella barbara* Linnaeus, 1758.
- 1924 *Patellanax* Iredale, Proceedings of the Linnean Society of New South Wales, volume 49, part 3, p. 239. Type, by original designation: *Patella squamifera* Reeve, 1855.
- 1929 *Penepatella* Iredale, Memoirs of the Queensland Museum, volume 9, part 3, p. 276. Type, by original designation: *Penepatella inquisitor* Iredale, 1929.

Patella argenvillei Krauss, 1848

(Pl. 65, fig. 4; Pls. 93, 96)

Range—South Africa: Port Nolloth on the west coast, eastward to Qolora, between East London and Durban.

Remarks—This species is more common on the west coast where it forms concentrated low-tidal communities, termed the Cochlear-argenvillei zone. It is one of the least variable of South African lim-

pets, easily recognised by its narrowly elongate-oval, high-conical form, dense regular sculpture, and dark external coloration, with white linear rib interstices.

Description—Shell large, up to 89 mm. (3½ inches) in length, rather solid, oblong-ovate, slightly constricted at the anterior end, high conical, with the apex subcentral, a little nearer to the anterior end. Sculpture consisting of very numerous, over 100, more or less regular, flat-topped radial ribs, with linear interstices; margin delicately and evenly crenulated. Colour: externally blackish, the rib interstices white; internally white, dark-greyish between the marginal crenulations, and spatula diffused with yellowish brown.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Central teeth consisting of a narrow insignificant middle member, with a pair of strong, sharply-cusped and centrally-grooved teeth on each side; lateral massive, with an expanded top, bearing four sharp cusps, the middle two deeply grooved; marginals three, weakly cusped and slender.

Measurements (mm.).—

length	width	height	
89.0	68.0	52.0	Table Bay
77.0	58.0	35.5	South Africa
63.0	44.5	30.0	Port Elizabeth

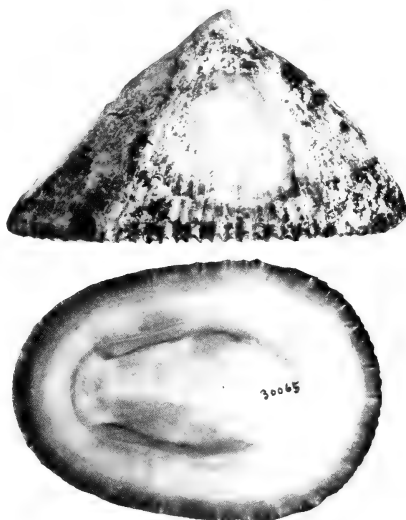


Plate 93. *Patella (Scutellastra) argenvillei* Krauss, 1848. Port Alfred, South Africa, 72-77 mm., AWBP coll. 30065.

Synonymy—

- 1848 *Patella argenvillei* Krauss, Sudafr. Moll., Stuttgart, p. 49; based upon Argenville Conch., 1870, vol. 1, p. 504 and vol. 3, pl. 3, fig. G.
 1854 *Patella argenvillei* Krauss, Reeve, Conch. Iconica, pl. 10, figs. 20a, b.
 1891 *Patella (Scutellastra) argenvillei* Krauss, Pilsbry, Man. Conch., vol. 13, p. 95, pl. 22, figs. 15, 16; pl. 58, fig. 44.
 1949 *Patella argenvillei* Krauss, Koch, Ann. Natal Mus., vol. 11(3), p. 494, pl. 17, figs. 1-3; text figs. 1, 2 (radula).

Records—SOUTH AFRICA: Table Bay (AWBP coll.); False Bay (AWBP coll.); Sea Point (Mrs. N. Prior); Port Elizabeth (Auck. Mus.); Port Alfred (AWBP coll.).

***Patella barbara* Linnaeus, 1758**

(Pl. 65, figs. 1-3; Pls. 94-96)

Range—South Africa, the whole length of the coastline from Port Nolloth in the west to Umpan-gazi in the east.

Remarks—This is a large, solid, ovate limpet, varying greatly in height, but always strongly radially ridged, resulting in a deeply corrugated margin. The coloration is buff to pale brownish externally and white within, except for the spatula, which is often blotched with reddish brown.

Description—Shell rather large, up to 95 mm. (3½ inches) in length, of only moderate height and weight in its younger stages but tall and crass in mature examples, narrowly to broadly ovate, with the apex near central. Sculpture variable, but always strongly and coarsely radially ribbed, their terminal points corrugating the margin, sometimes almost as

strongly as in *longicosta*. Radial ribs carinated and of varying strength, from 10 to 20 primaries and 1 to 4 secondaries in the interspaces, the whole rendered noticeably scabrous by close set, lamellose, concentric growth marks. The posterior end of the shell usually has 5 ribs much stronger than the rest. Colour: externally dull-buff to light yellowish brown; internally whitish, often with a narrow, pale-fawn, marginal border; spatula either irregularly blotched with reddish-brown, or callused over with white. A variable species, as shown by the lengthy synonymy.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3, similar to that of both *longicosta* and *cochlear* in the form of the massive lateral, which has an expanded head, bearing three cusps, the middle one much the larger, and there is an incipient fourth cusp on the outer side. The five centrals have the middle member small and slender, with a minute vestigial cusp, but the cusps of the outer pairs of centrals, and the middle member of the laterals have broad flat tops, with ridged margins; marginals 3, slender, flexuous, and each with a weak cusp.

Measurements (mm.)—

length	width	height	
95.0	81.0	37.0	Buluga Bay, East London;
			Mrs. N. Prior
95.0	70.0	31.0	var. <i>ovalis</i> Pilsbry, 1891, p. 97
84.5	61.5	31.5	Still Bay
79.0	58.0	38.0	C. of Good Hope
79.0	62.0	22.5	Port Alfred
72.0	60.0	27.0	Pilsbry, 1891, p. 96

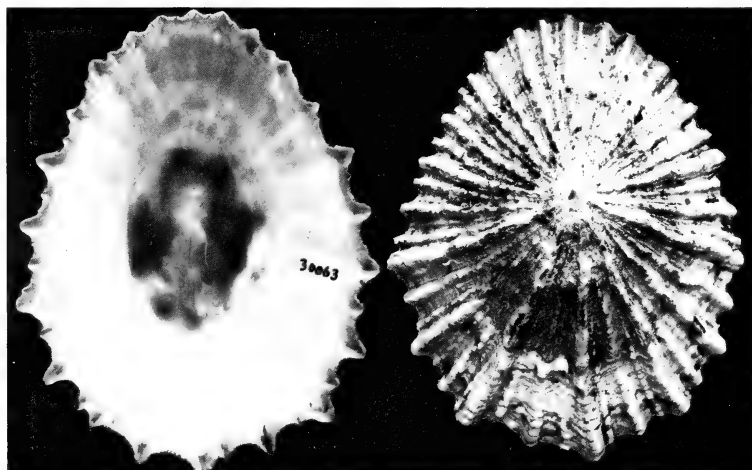


Plate 94 *Patella (Scutellastra) barbara* Linnaeus, 1758, Port

Alfred, South Africa, 76 mm., AWBP coll. 30063.

Synonymy—

- 1758 *Patella barbara* Linnaeus, Syst. Nat., ed. 10, p. 782.
 1778 *Patella plicata* Born, Mus. Caes. Vind., p. 433; 1780, Test. Mus. Caes. Vind., p. 417, pl. 18, fig. 1.
 1786 *Patella fungoides* Lightfoot, Cat. Portland Mus., p. 55.
 1786 *Patella gorgonica* Lightfoot, Cat. Portland Mus., p. 105.
 1791 *Patella phicaria* Gmelin, Syst. Nat., ed. 13, p. 3708.
 1791 *Patella cypria* Gmelin, Syst. Nat., ed. 13, p. 3698.
 1819 *Patella barbata* Lamarck, Anim. sans vert., vol. 6 (1), p. 326.
 1819 *Patella spinifera* Lamarck, Anim. sans vert., vol. 6 (1), p. 326.
 1848 *Patella barbara* L., Krauss, Sudafr. Moll., Stuttgart, p. 45.
 1848 *Patellaa obiecta* Krauss, Sudafr. Moll., Stuttgart, p. 47, pl. 3, fig. 11.
 1851 *Patella plicata* Born, Reeve, Conch. Iconica, pl. 9, figs. 16a, b.
 1891 *Patella (Scutellastra) barbara* L., Pilsbry, Man. Conch., vol. 13, p. 96, pl. 15, figs. 1, 2; pl. 59, figs. 50-55.
 1891 *Patella (Scutellastra) barbara* var. *ovalis* Pilsbry, Man. Conch., vol. 13, p. 97, pl. 60, figs. 56-58.
 1932 *Patella barbara* L., Turton, Mar. Shells Port Alfred, sp. 162.
 1932 *Patella barbara plicata* Born, Turton, Mar. Shells Port Alfred, p. 163.
 1932 *Patella whitechurchi* Turton, Mar. Shells Port Alfred, p. 164, pl. 37, fig. 1165.
 1932 *Patella thetis* Turton, Mar. Shells Port Alfred, p. 164, pl. 37, fig. 1166.
 1932 *Patella hera* Turton, Mar. Shells Port Alfred, p. 164, pl. 37, fig. 1167.
 1932 *Patella amphitrite* Turton, Mar. Shells Port Alfred, p. 164, pl. 37, fig. 1168.
 1932 *Patella amphitrite* var. *brunescens* Turton, Mar. Shells Port Alfred, p. 164, pl. 37, fig. 1169.
 1932 *Patella decemcostata* var. *major* Turton, Mar. Shells Port Alfred, p. 165, pl. 38, fig. 1171.
 1932 *Patella nympha* Turton, Mar. Shells Port Alfred, p. 165, pl. 38, fig. 1174.
 1932 *Patella sowerbyi* Turton, Mar. Shells Port Alfred, p. 166, pl. 38, fig. 1176.

1949 *Patella barbara* Linne, Koch, Ann. Natal Mus., vol. 11 (3), p. 496, pl. 18, figs. 1-12; text figs. 3a, b, 4 (radula).

Records—SOUTH AFRICA: whole length of coastline from west to east (Koch, 1949, p. 496); Table Bay (Auck. Mus. 3081); Cape of Good Hope; Still Bay; False Bay; Port Alfred; Cape Natal (all AWBP coll.).

Patella longicosta Lamarck, 1819

(Pl. 65, figs. 5-7; Pls. 95, 96)

Range—South Africa, from Oudekraal, west side of Cape Peninsula, eastward to Umpangazi, north of Durban.

Remarks—This species is easily recognised by its depressed star-shape, with the primary ribs extending well-beyond the margin, which is narrowly bordered in black. This species occurs commonly in the lower Balanoid and Cochlear zones.

Description—Shell rather large, up to 76 mm. (3 inches) in length, solid, depressed, stellate, very strongly sculptured with sharply carinated, radial ridges, that project well-beyond the margin, seven of them much stronger than the rest; apex at anterior third to submedian. Colour of exterior dull-black, when not eroded, to a rusty-brown; interior bluish white, with a narrow black margin, and a yellowish brown spatula, the latter clouded with a white callus in senile specimens.

Radula—Formula $3+1+(2+1+2)+1+3$, somewhat similar to that of *cochlear* in the form of the cusps, which are leaf-shaped with a median groove, and in the massive lateral that has four cusps.

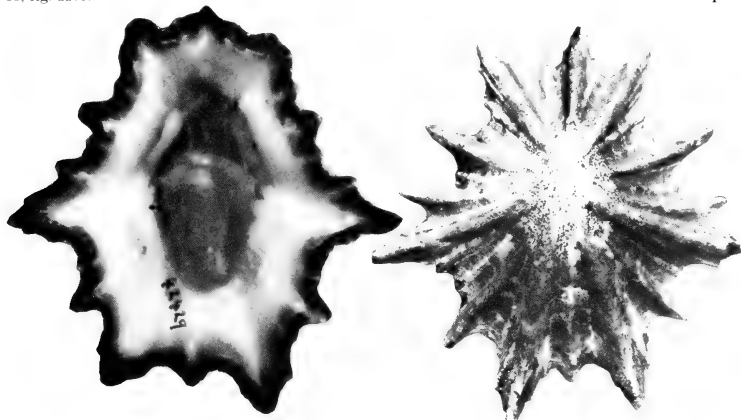


Plate 95. *Patella (Scutellastra) longicosta* Lamarck, 1819. Mossel Bay, Cape Peninsula, South Africa, 66 mm., AWBP

coll. 42429.

Measurements (mm.)—

length	width	height	
75.5	75.5	23.0	False Bay
70.0	64.0	18.0	False Bay
61.0	56.0	12.0	Cape Peninsula

Synonymy—

- 1819 *Patella longicosta* Lamarck, Anim. sans vert., vol. 6 (1), p. 326.
 1842 *Patella longicosta* Lam., Reeve, Conch. Syst., vol. 2, p. 15, pl. 136, fig. 6.
 1848 *Patella longicosta* Lam., Krauss, Sudafr. Moll., Stuttgart, p. 48.
 1854 *Patella longicosta* Lam., Reeve, Conch. Iconica, pl. 6, figs. 11a, b.
 1891 *Patella (Scutellastra) longicosta* Lamarck, Pilsbry, Man. Conch., vol. 13, p. 107, pl. 28, figs. 37, 38.

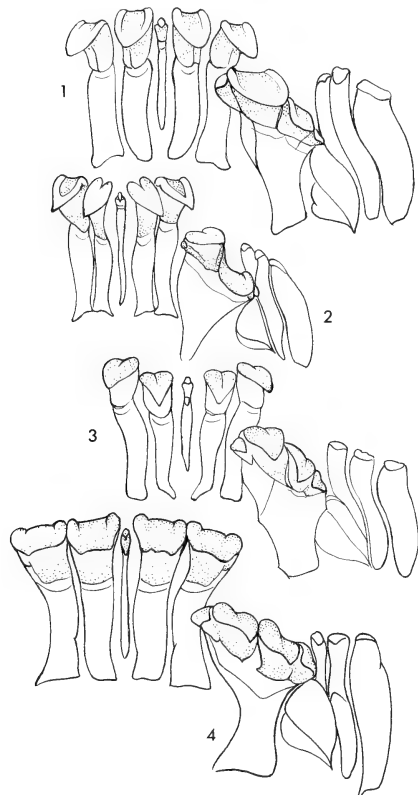


Plate 96. Fig. 1. Radula of *Patella (Scutellastra) barbara* Linnaeus. Fig. 2. *Patella (Scutellastra) longicosta* Lamarck. Fig. 3. *Patella (Scutellastra) argentei* Krauss. Fig. 4. *Patella (Scutellastra) tabularis* Krauss. South Africa. Radulae, all from Koch, 1949.

- 1901 *Patella decemcostata* E. A. Smith, Journ. Conch., vol. 10, p. 106, pl. 1, fig. 22.
 1932 *Patella longicosta* Lam., Turton, Mar. Shells Port Alfred, p. 161, pl. 37, fig. 1145.
 1932 *Patella longicosta intermedia* Turton, Mar. Shells Port Alfred, p. 161, pl. 37, fig. 1146.
 1932 *Patella multilirata* Turton, Mar. Shells Port Alfred, p. 161, pl. 37, fig. 1147.
 1932 *Patella tabularis* Krauss, Turton, Mar. Shells Port Alfred, p. 161. (non Krauss, 1848; in part, smaller of two examples).
 1932 *Patella tabularis angulosa* Gmelin, Turton, Mar. Shells Port Alfred, p. 161, sp. 1150. (non Gmelin, 1791).
 1932 *Patella tabularis monopsis* Gmelin, Turton, Mar. Shells Port Alfred, p. 162. (sic; non *monopsis* Gmelin, 1792).
 1932 *Patella tabularis squamosa* Gmelin, Turton, Mar. Shells Port Alfred, p. 161, sp. 1149. (non Gmelin, 1791).
 1932 *Patella granatina* Linn. Turton, Mar. Shells Port Alfred, p. 163, sp. 1161. (non Linnaeus, 1758).
 1932 *Patella decemcostata* E. A. Smith, Turton, Mar. Shells Port Alfred, p. 165.
 1932 *Patella albaniana* Turton, Mar. Shells Port Alfred, p. 165, pl. 38, fig. 1175.
 1933 *Patella longicosta kowiensis* Turton, Journ. Conch., vol. 19, p. 371; nom. nov. pro *P. longicosta intermedia* Turton, 1932, non Knapp, 1857.
 1942 *Patella longicosta* Lam., Tomlin and Stephenson, Proc. Malac. Soc., Lond., vol. 25, pp. 4-9.
 1949 *Patella longicosta* Lam., Koch, Ann. Natal Mus., vol. 11 (3), p. 504, pl. 20, figs. 6-13; text figs. 13a-c, 14 (radula).

Records—SOUTH AFRICA: Cape Peninsula (AWBP coll.); Kommetje, Cape Peninsula (Mrs. N. Prior); Mossel Bay, Cape Peninsula (V. Orr, 1955; ANSP); False Bay (AWBP coll.); Still Bay (Auck. Mus.); Simon's Bay (V. Orr, 1955; ANSP); Port Elizabeth (Auck. Mus.); Cape Natal (AWBP coll.); Port Alfred (AWBP coll.).

Types—The type series of three examples of *longicosta* is in the Muséum D'Histoire Naturelle de Genève.

***Patella tabularis* Krauss, 1848**

(Pl. 66, fig. 5; Pls. 96, 97)

Range—South Africa, from Cape Peninsula eastward to Port St. John's.

Remarks—This is the largest of the South African limpets; it somewhat resembles *kermadecensis* but has much more prominent radial sculpture. The species inhabits the sub-littoral fringe, and does not occur in dense communities (Koch, 1949, p. 509).

Description—Shell very large and massive, up to 147.5 mm. (5¾ inches) in length, broadly ovate, moderately elevated, and with the apex anterior to the middle. Sculpture heavy and coarse, consisting of 9, 10 or more heavy, foldlike, radial ribs, and numerous secondary ribs of several sizes, the whole imbricated by dense lamellose growth lines; margin deeply and somewhat irregularly scalloped. Colour: exterior dull reddish or rusty-brown; interior porcelainous-white, with a moderately wide border of reddish brown, being the external colour showing through at the thinner margin; spatula not differentiated by colour.

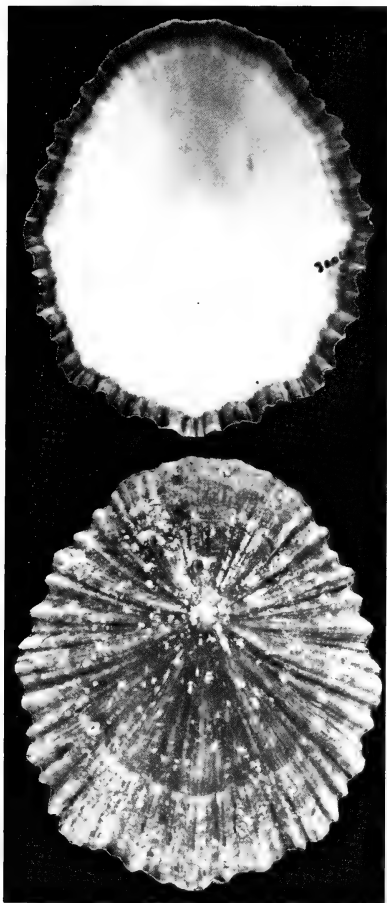


Plate 97. *Patella (Scutellastra) tabularis* Krauss, 1848. Port Alfred, South Africa, 115 mm., AWBP coll. 30062.

Measurements (mm.)—

length	width	height	
147.5	125.5	50.0	Buluga Bay, East London; Mrs. N. Prior
127.0	111.9	46.0	South Africa
114.0	98.0	32.0	Cape Point
81.0	68.0	20.5	Port Alfred

Radula—Formula $3 + 1 + (2+1+2) + 1 + 3$. Central teeth consisting of a slender, almost vestigial, middle member, flanked by pairs of large, blunt-cusped

teeth; lateral massive, with an expanded head, bearing four cusps, the middle pair the stronger; marginals three, narrow and slender, each with a weak cusp.

Synonymy—

- 1848 *Patella tabularis* Krauss, Südafr. Moll., Stuttgart, p. 47, pl. 3, fig. 8.
 1854 *Patella rustica* L., Reeve, Conch. Iconica, pl. 5, figs. 8a, b. (non Linnaeus, 1758).
 1891 *Patella (Scutellastra) tabularis* Krauss, Pilsbry, Man. Conch., vol. 13, p. 105, pl. 16, figs. 9, 10.
 1891 *Patella (Scutellastra) patriarcha* Pilsbry, Man. Conch., vol. 13, p. 105, pl. 64, figs. 84, 85; pl. 65, fig. 86.
 1932 *Patella rustica* L. Turton, Mar. Shells Port Alfred, p. 162, sp. 1154.
 1932 *Patella tabularis* Krauss, Turton, Mar. Shells Port Alfred, p. 161, sp. 1148 (in part; larger of two specimens).
 1932 *Patella obtecta* Krauss Turton, Mar. Shells Port Alfred, p. 162, sp. 1155. (non Krauss).
 1932 *Patella patriarcha* Pilsbry, Turton, Mar. Shells Port Alfred, p. 162, sp. 1153.
 1942 *Patella tabularis* Krauss Tomlin and Stephenson, Proc. Malac. Soc., Lond. vol. 25 (1), p. 5.
 1949 *Patella tabularis* Krauss, Koch, Ann. Natal Mus., vol. 11 (3), p. 509, pl. 22, figs. 5-11; text figs. 19a, b, 20 (radula).

Types—The type of *tabularis* is in the Stuttgart Museum, formerly the Naturalien Cabinet.

Records—SOUTH AFRICA: Cape Peninsula to Port St. John's (Koch, 1949, p. 509); Cape Point (AWBP coll.); Port Alfred (AWBP coll.); Buluga Bay, East London (Mrs. N. Prior).

Patella exusta Reeve, 1854

(Pl. 98, fig. 1; Pl. 104, fig. 3)

Range—Mauritius.

Remarks—The typical subspecies seems to be confined to Mauritius, although the wider-ranging subspecies *pica* Reeve, sometimes occurs along with it. The distinctive character of *exusta* is the dull-black, thick outer layer of the shell, which also produces the narrow, black internal border. It is unfortunate that the better known name, *chitonoides* has to fall as a synonym of *exusta*.

Description—Shell of moderate size, up to 54 mm. (2½ inches) in length, solid, rather depressed, elongate-ovate, and decidedly narrowed anteriorly. Apex subcentral to about the anterior third. Sculpture consisting of about 20 narrow sharply raised primary radial ribs, and 3 or 4 weak radial threads in the wider interspaces, over the posterior half of the shell. The margin is broadly and shallowly corrugated. Colour of exterior, when not encrusted or abraded, uniformly dull black; interior pale bluish to pinkish white, with a narrow black margin. The spatula is weakly defined, and sometimes partly clouded by a pale fawn callus.

Measurements (mm.)—

length	width	height	
54.0	38.0	13.0	syntype of <i>chitonoides</i>
53.0	44.0	14.0	lectotype of <i>exusta</i>
48.0	38.0	16.0	Mauritius
47.0	37.75	11.5	lectotype of <i>chitonoides</i>
45.0	35.0	12.5	Mauritius

Synonymy—

- 1854 *Patella exusta* Reeve, Conch. Iconica, pl. 15, figs. 35a, b. (locality unknown).
 1854 *Patella chitonoides* Reeve, Conch. Iconica, pl. 21, figs. 52a, b. (locality unknown). Dec. 1854.
 1891 *Patella (Scutellastra) exusta* Reeve, Pilsbry, Man. Conch., vol. 13, p. 98, pl. 24, figs. 9, 10.
 1891 *Patella (Scutellastra) pica* form *chitonoides* Reeve, Pilsbry, Man. Conch., vol. 13, p. 98, pl. 26, figs. 28, 29.

Types—The types of both *exusta* and of *chitonoides* are in the British Museum (Natural History). That of *exusta* consists of three syntypes glued to a tablet. One of these, measuring 53 x 44 x 14 mm., matches Reeve's figure, pl. 15, fig. 35, and is here nominated lectotype. The other two specimens on the tablet are the Californian *Acmaea pelta* Eschscholtz, and may have been added later than Reeve. The type series of *chitonoides* also consists of three syntypes, and the one matching Reeve's fig. 52,

measuring 47 x 37.75 x 11.5 mm. is here nominated lectotype.

Records—Locality unknown for the types of both *exusta* and *chitonoides*. MAURITIUS: (AWBP coll.); Vacoas Point, 3 miles south of Mahebourg (Ruth Ostheimer and Virginia Orr, Nov. 20, 1960).

***Patella exusta*
subspecies *pica* Reeve, 1854**

(Pl. 98, figs. 2-4)

Range—Islands of the Indian Ocean, Mauritius to Seychelles.

Description—Shell of similar size and shape to *exusta* typical, being elongated and noticeably narrowed anteriorly, but the coloration is different, for instead of the whole of the outer surface being black, that colour is confined to radiate lines or streaks, often short and intermittent, and present only in the primary rib interstices, the rest of the exterior of the shell being white. Internally the shell is porcellaneous-white with the spatula irregularly stained orange-brown, and at the margin the dark external pattern shows through, forming an intermittent narrow border.

Measurements (mm.)—

length	width	height	
49.5	38.00	14.0	lectotype
47.0	37.25	10.0	Mauritius
44.5	36.25	10.5	Mahe, Seychelles
38.0	30.00	6.5	Mauritius
30.4	26.00	5.0	Seychelles

Synonymy—

- 1854 *Patella pica* Reeve, Conch. Iconica, pl. 19, figs. 45a-c.
 1891 *Patella (Scutellastra) pica* Reeve, Pilsbry, Man. Conch., vol. 13, p. 97, pl. 22, figs. 9, 10, 13, 14; pl. 59, figs. 47-49 (not pl. 26, figs. 28, 29).
 1863 *Patella moreli* Deshayes, Cat. Moll. Réunion, p. 43, pl. 6, fig. 13.
 1863 *Patella levata* Deshayes, Cat. Moll. Réunion, p. 44, pl. 6, fig. 14.

Records—"South Seas" (type); MAURITIUS: (AWBP coll.); Vacoas Point, 3 miles south of Mahebourg (Ruth Ostheimer and Virginia Orr, Nov. 20, 1960). SEYCHELLES: (AWBP coll.); Mahé (AWBP coll.); Frigate Island (AWBP coll.). REUNION: (Deshayes, 1863).

Types—The type series of *pica* is in the British Museum (Natural History) and consists of three syntypes mounted upon a tablet. The one measuring 49.5 x 38 x 14 mm. is here nominated lectotype.

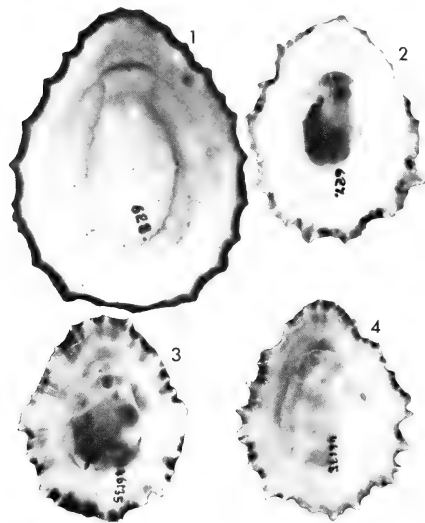


Plate 98. Fig. 1. *Patella (Scutellastra) exusta* Reeve, 1854. Mauritius, 48 mm., AWBP coll. 628. Figs. 2-4 *Patella (Scutellastra) exusta* subspecies *pica* Reeve, 1854. Fig. 2. Mauritius, 38 mm., AWBP coll. 627. Figs. 3,4. Mahé, Seychelles, 42-45 mm., AWBP coll. 46135.

Patella flexuosa Quoy and Gaimard, 1834

(Pl. 65, figs. 8, 9; Pls. 99, 104)

Range—Andaman Islands and the tropical Pacific as far east as the Tuamotu Islands.

Remarks—This exceedingly variable species has had many names, and unfortunately the one under which it has usually appeared, *stellaeformis* Reeve, 1842, must fall as a synonym of the earlier *flexuosa* Quoy and Gaimard, 1834.

The species is intertidal and a shallow-water dweller, living attached to coral rock, or sometimes upon the outer and inner surfaces of large shells. Examples living attached to shells tend to be of lighter build, and of more circular outline

than those from coral-rock faces, but that is not invariably so, and all manner of shapes, sculpture and coloration is encountered, irrespective of station.

The species varies between 14 mm. and 41 mm., is circular to elongate-ovate in shape, may be almost flat to moderately elevated, thin or solid. The strength of the external ribbing determines the degree to which the margin is scalloped. The exterior is dull-white, sometimes sparingly speckled, lined, or with zigzag dark-brown markings in the rib interstices, but the outer surface is usually lime-encrusted. The interior is porcellaneous, more or less white, and the spatula

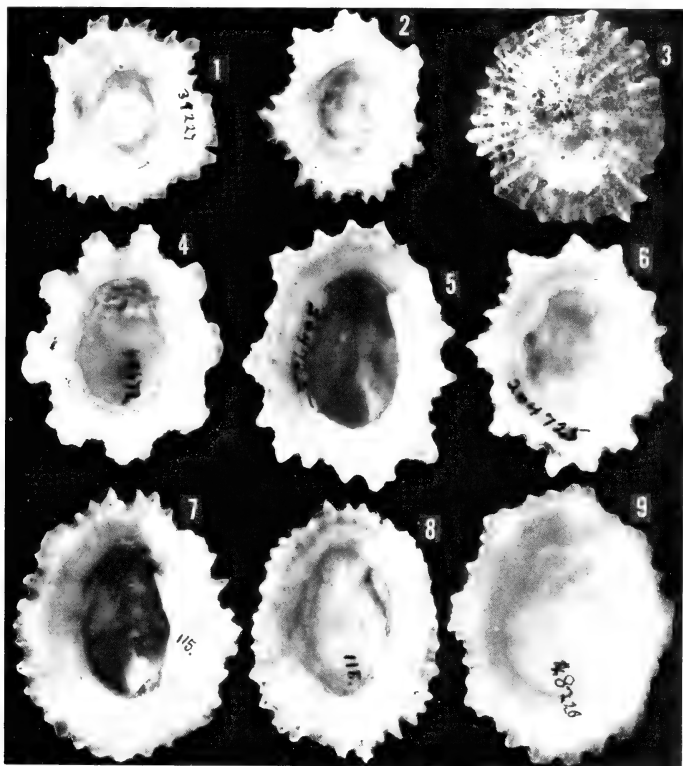


Plate 99. Figs. 1-9. *Patella* (*Scutellastra*) *flexuosa* Quoy & Gaimard, 1834. Fig. 1. Rorua Island, Aorai Islands, West New Guinea (*stellaeformis* form), 30 mm., AWBP coll. 39227. Figs. 2, 3. Michaelmas Cay, off Cairns, North Queensland, 29-34 mm. (topotypes of *inquisitor*), AWBP coll. 46062.

Fig. 4. New Caledonia, 31 mm. (topotype of *intraurea*), AWBP coll. 45672. Figs. 5, 6. Wake Island, 31-34 mm., AWBP coll. 204725. Figs. 7, 8. Paia, Tahiti, Society Islands, 33-35 mm. (*paumotuensis* form), AWBP coll. 115. Fig. 9. Bikini Island, Marshall Islands, 35 mm., AWBP coll. 48226.

may be white, yellowish, orange-brown, or sometimes dark-slate.

Description—Shell rather small, up to 42 mm. (1½ inches) in length, typically roundly-octagonal, with the apex nearly central, sculptured with 8 or 9 rounded radial folds that project strongly at the margin. The entire surface, folds and interstices alike, is densely sculptured with secondary, crisp, scabrous to spinose cords. In some forms the primary and secondary radials become nearly equal, in which cases the octagonal outline is modified to a crenulated oval. Colour as described under remarks.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3, very similar to that of *exusta pica* and *kermadecensis*. Prashad and Rao figured the radula of their 'tara,' which compares closely with the radula of a Cook Islands specimen. Prashad and Rao considered their species to be related to the South African *granularis*, but in that species the cusps are better formed, parrot-beaklike, and the shell is quite unlike the *flexuosa* group in form, size, texture and coloration.

Measurements (mm.)—

length	width	height	
41.0	35.0	17.5	Fakarawa, Tuamotus
39.0	30.0	9.5	Tokorava, Tuamotus
33.0	30.0	8.0	Michaelmas Cay (type of <i>inquisitor</i>)
30.0	28.0	9.0	Aoeri Ids., W. New Guinea
22.5	—	—	Vanikoro Id. (type of <i>flexuosa</i>), 10 lignes.
16.0	15.0	11.0	Michaelmas Cay (type of <i>arrecta</i>)
14.0	12.0	3.5	Andaman Islands (type of <i>tara</i>)

Synonymy—

- 1834 *Patella flexuosa* Quoy & Gaimard, Voy. Astrolabe, Zool., vol. 3, p. 344, pl. 70, figs. 9-11.
 1842 *Patella stellaeformis* Reeve, Conch. Syst., vol. 2, p. 15, pl. 136, fig. 3.
 1846 *Patella paumotensis* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 150.
 1854 *Patella pentagona* Born, Reeve, Conch. Iconica, pl. 20, figs. 48a-c.
 1854 *Patella cretacea* Reeve, Conch. Iconica, pl. 21, figs. 53a, b.
 1891 *Patella stellaeformis* Reeve, Pilsbry, Man. Conch., vol. 13, p. 98, pl. 17, figs. 25-27; pl. 61, figs. 62-65.
 1891 *Helcioniscus flexuosus* Q. and G., Pilsbry, Man. Conch., vol. 13, p. 130, pl. 66, figs. 96-98.
 1929 *Penicopatella inquisitor* Iredale, Mem. Queensl. Mus., vol. 9, pt. 3, p. 276, pl. 31, figs. 17, 18.
 1929 *Penicopatella arrecta* Iredale, Mem. Queensl. Mus., vol. 9, pt. 3, p. 276, pl. 31, figs. 21, 22.
 1929 *Penicopatella intraurea* Iredale, Mem. Queensl. Mus., vol. 9, pt. 3, p. 276.
 1933 *Patella (Scutellastra) stellaeformis tuamotuensis* Dautzenberg & Bouge, Journ. Conchyl., vol. 77, p. 417; emendation pro *paumotensis* Gould, 1846.
 1934 *Patella (Patellidea) tara* Prashad & Rao, Rec. Indian Mus., vol. 36 (1), p. 1, pl. 1, figs. 1a-c, 2.

Types—The type of *flexuosa* should be in the Museum National d' Histoire Naturelle, Paris; three syntypes of *cretacea* are in the British Museum (Natural History); two syntypes of *paumotensis* are in the United States National Museum; the holotypes of *inquisitor*, *arrecta* and *intraurea* are in the Australian Museum, Sydney, and the holotype of *tara* is in the Indian Museum, Calcutta.

Records—ANDAMAN ISLANDS: S. Corbyn's Cove, Port Blair, on *Trochus niloticus* Linn. (Prashad & Rao). INDONESIA: Keledjitan, Bantam, Java (USNM). WEST NEW GUINEA: reef off Rouw Island, Aoeri Islands (ANSP. Exped., 24 Feb.



Plate 100. Figs. 1, 2. *Patella (Scutellastra) flexuosa* sub-species *optima* Pilsbry, 1927. Fig. 1. Osuni, Japan, 93.5 mm., AWBP coll. 344004. Fig. 2. Waki, Satsuma, Japan, 48 mm., AWBP coll. 204724.

1956; AWBP coll.); Pai Island, Mios Woendi, Padaido Islands (ANSP). PHILIPPINES: Talin Bay, Batangas, Luzon (ANSP); Iba, Zambales, Luzon (ANSP). PALAU ISLANDS: Eil Malk Island (ANSP). MARIANAS: Guam, Saupon Point (AWBP coll.); Port Merizo (ANSP); Lagunan Tanapag, Saipan (ANSP). WAKE ISLAND: (ANSP); (AWBP coll.). LINE ISLANDS: Palmyra Island (USNM); (Bishop Mus.); (AWBP coll.); Washington Island (Bishop Mus.); Christmas Island (Bishop Mus.); Jarvis Island (ANSP). MARSHALLS: Enyu Island, Bikini (USNM); N.W. end Bikini Island (USNM); Kabelle Island, Rongelap (USNM); Wotho Island (USNM). SOLOMON ISLANDS: Bumana (AWBP coll.); Malaita Island (AWBP coll.). SANTA CRUZ ISLANDS: Vanikoro (type of *flexuosa*). NEW HEBRIDES: Pango Point, S. W. Efate, intertidal, on coral (W. O. Cernohorsky, 3-9-1970). N. W. AUSTRALIA: near Broome (Aust. Mus.). NORTH QUEENSLAND: Piper Island (Aust. Mus.); Masthead Reef (Aust. Mus. C. 18967); Michaelmas Cay, off Cairns, on or inside of *Tridacna* shells (types of *inquisitor* and *arrecta*; Aust. Mus.). NEW CALEDONIA (type of *intraurea*; Aust. Mus.); (AWBP coll.). LOYALTY ISLAND: (AWBP coll.); Lifu Island (ANSP). FIJI ISLANDS: fringe reef, Korolevu, Viti Levu Island (ANSP). TONGA ISLANDS: (AWBP coll.). SAMOA: Pango Harbor (Aust. Mus.); Niuafofua Island (USNM); Ofu Island (ANSP); (AWBP coll.). COOK ISLANDS: Rarotonga (AWBP coll.); outer reef, near Muri, Rarotonga (L. Price, 1965). AUSTRAL ISLANDS: Rurutu Island (ANSP). SOCIETY ISLANDS: Tahiti (type of *cretacea*); Paee (AWBP coll.); Atiue District, Punaauia, seaward edge of reef (R. Robertson, 1952; ANSP); S. W. of Tautira Village (ANSP). TUAMOTU ARCHIPELAGO: Fakarava Island (USNM); (AWBP coll.); Tokorava Island (AWBP coll.); Raroia Island (ANSP); Makatea Island (USNM).

***Patella flexuosa*
subspecies *optima* Pilsbry, 1927**

(Pl. 65, fig. 10; pl. 100)

Range—Japan, Amami Islands and Ryukyu Islands.

Remarks—This shell, here considered to be a

temperate subspecies of the tropical *flexuosa*, is extremely depressed, especially in its juvenile form, and at all stages of growth the prominent marginal lobes are a characteristic. Also, it attains a very much larger adult size than any other form of *flexuosa*.

Description—Shell large, up to 93.4 mm. (3½ inches) in length, solid, very depressed, elongate-ovate, gradually narrowed in front, apex varying between subcentral and the anterior third. Sculpture consisting of from 9 to 11 broad radial folds, that give a prominently lobed outline to the margin. The whole surface is crowded with narrow rounded radials that are rendered scabrous by concentric growth lines. Colour of exterior greyish to pale orange, with maroon to dark purplish-brown stripes in the interspaces of the radial folds. Interior porcellaneous-white, the spatula clouded here and there with cinnamon-brown. Margin of shell with a narrow, semitransparent amber-coloured border, showing brownish maculations corresponding to the external pattern.

Measurements (mm.)—

length	width	height	
93.5	70.0	16.0	Osumi, Japan
92.0	72.0	16.0	Kakushima, Japan
84.0	60.0	15.0	holotype
56.0	41.5	8.0	Waki, Japan
40.0	32.5	5.0	Waki, Japan

Synonymy—

1927 *Patella stellaeformis optima* Pilsbry, The Nautilus, vol. 40, no. 4, p. 138, not figured.

1964 *Penepatella optima* Pilsbry, Habe, Shells of Western Pacific in colour, vol. 2, p. 7, pl. 3, fig. 1.

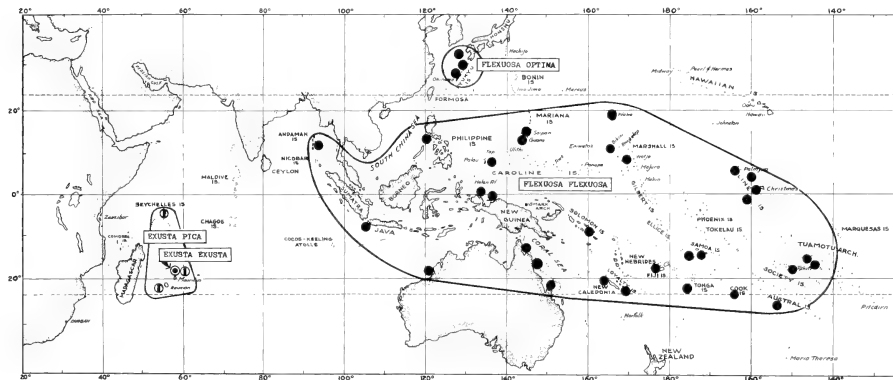


Plate 101. Geographical distribution of *Patella* (*Scutellastra*) *exusta* Reeve, *Patella* (*Scutellastra*) *exusta* subspecies *pica*

Reeve, *Patella* (*Scutellastra*) *flexuosa* Quoy & Gaimard, and *Patella* (*Scutellastra*) *flexuosa* subspecies *optima* Pilsbry.

Records—JAPAN: Yakushima, Osumi (type); Suwanosejima, Osumi (AWBP coll.); Waki, Kyushu Island (AWBP coll.). Amami and Ryukyu Islands (Habe, 1964).

Types—The holotype is in the Academy of Natural Sciences of Philadelphia. No. 98023.

***Patella kermadecensis* Pilsbry, 1894**

(Pl. 66, fig. 1; Pls. 102-104)

Range—Kermadec Islands

Remarks—This species is restricted to the Kermadec group, and is the second largest known living member of the Patellidae, sometimes attaining a length of seven inches, and exceeded in size only by the tropical West American *Patella* (*Ancistromesus*) *mexicana*.

The white porcellaneous interior, and orange border of the shell, as well as its broadly ovate shape, readily distinguish *kermadecensis*.

Description—Shell very large and massive, up to 174 mm. (6½ inches) in length, broadly ovate, but slightly narrowed in front, apex almost central, and dorsal slopes almost straight. Sculpture consisting of a dense coverage of narrow radial ribs, all rendered weakly scabrous by concentric growth lines. The primary radials number from 35 to 50, and the secondary ones, which are almost as strong, number from 3 to 5 for each interspace. The margin is broadly and shallowly scalloped, corresponding to the interspaces of the primary radials. Colour of exterior dull-orange; interior porcellaneous-white, with a narrow margin, that varies from pale to bright orange, and very occasionally is dark greenish-brown. The muscle impression is mostly dull cream, but occasionally it is greenish. Young shells have the

spatula fawn to pale orange-brown, and the orange border to the shell, varying from plain orange or radially streaked to almost continuously blotched with brown. The greenish muscle impression is present only in shells that have been thinned by external erosion.

Radula—Formula $3 + 1 + (2 + 1 + 2) + 1 + 3$. Radula very short and folded back upon itself at the end, as in typical *Patella*. There are five central teeth in a horizontal row, the median one shorter, narrower, and much smaller than the other four; all five bear blunt chisel-shaped cusps. The lateral is massive, with a broad head, bearing three fused chisel-shaped cusps. The three semitransparent marginals are small, elongated and narrow, each with a small blunt cusp.

Animal—As in *Patella vulgata*, the gill cordon is continuous, not interrupted by the head as in *Cellana*, and the cephalic tentacles are short and broadly conical, with the eye in a pit at the outer base.

Measurements (mm.)—

length	width	height	
174.0	160.0	—	Oliver, 1915, p. 510
153.0	137.0	51.0	Raoul Island
148.5	135.0	50.0	Raoul Island
136.0	117.0	42.0	Raoul Island
123.5	108.0	30.5	Raoul Island

Synonymy—

- 1894 *Patella* (*Scutellastra*) *kermadecensis* Pilsbry, The Nautilus, vol. 7, p. 109.
 1894 *Patella kermadecensis* Pilsbry, Taylor, The Nautilus, vol. 7, p. 142.
 1894 *Patella pilsbryi* Brazier, Proc. Linn. Soc. N. S. W., vol. 9, ser. 2, p. 183 (disputed locality, substituted South Africa, and renamed species).



Plate 102. *Patella* (*Scutellastra*) *kermadecensis* Pilsbry, 1894.

Raoul Island, Kermadec Islands, 123.5 mm., AWBP coll. 207.

1894 *Patella kermadecensis* Pilsbry, Proc. Acad. Nat. Sci. Phila. pp. 208-212, pls. 7, 8 (Kermadec locality confirmed).

1895 *Patella (Scutellastra) kermadecensis* Pilsbry, Cheeseman, Proc. Linn. Soc. N. S. W., vol. 10, ser. 2, pp. 221-223 (Kermadec locality confirmed).

1902 *Patella kermadecensis* Pilsbry, Suter, Journ. Malac., vol. 9, p. 111, pl. 8 (animal and dentition).

1915 *Scutellastra kermadecensis* Pilsbry, Oliver, Trans. N. Z. Inst., vol. 47, p. 510.

Types—The type specimens are in the Academy of Natural Sciences of Philadelphia.

Records—KERMADEC ISLANDS: Raoul (Sunday Island) (type); Raoul, Macaulay, and Curtis Islands, also French Rock (Oliver, 1915); Raoul Island (Auck. Mus.); (AWBP coll.); north and east coasts of Raoul Island, also Meyer Islet (Cheeseman, 1895).

Patella aurorae Fleming, 1973

(Pl. 105)

Range—New Zealand; Mason River, north of Waiu, North Canterbury, in a boulder derived from the Isolated Hill Limestone of Duntroonian Oligocene age.

Remarks—This large and massive New Zealand fossil limpet is an obvious forerunner of the Recent *kermadecensis*, now confined to the Kermadecs, which is related to the Melanesian *tucupiana*. These isolated occurrences, both in time and in location, suggest that this group of limpets once had a considerable geographical range.

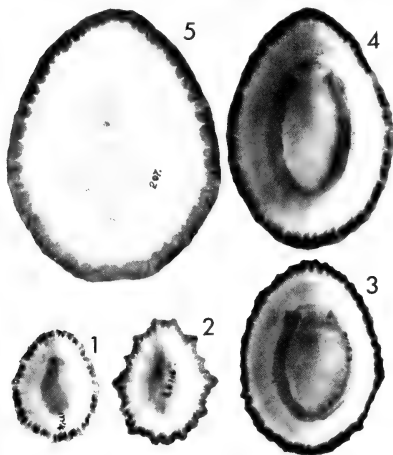


Plate 103. Figs. 1-5. *Patella (Scutellastra) kermadecensis* Pilsbry, 1894, Raoul Island, Kermadec Islands. Young stages in ascending order of size, from Fig. 1, length 30 mm. to Fig. 5, length 67 mm. Figs. 2 and 5 have a plain orange border. Figs. 1, 3 and 4 have the orange border streaked with dark brown. Figs. 3 and 4 are elevated, but Fig. 5 is very depressed. AWBP coll. 207, 17764 and 25116.

The Oligocene fossil, compared with the Recent *kermadecensis* is less noticeably narrowed in front, has the apex nearer to the anterior margin, and the sculpture is very much stronger.

These differences are here considered to warrant full specific, rather than subspecific status for *aurorae*.

Description—Shell very large and massive, up to 200 mm. (8 inches) in length, broadly ovate and moderately elevated, height a little less than one third that of the length. Sculpture coarse, consisting of about 32 strong primary radials and 4-6 secondary radials in each interspace. Apex about two fifths the length, from the anterior end, which is only slightly narrowed.

Measurements (mm.)—

length	width	height	
180	150	78	holotype
200	—	—	paratype

Types—Holotype and paratype in the collection of the New Zealand Geological Survey, Lower Hutt, Wellington.

Synonymy—

1973 *Patella (Scutellastra) kermadecensis aurorae* Fleming, N.Z. Journ. Mar. & Freshw. Res. vol. 7 (1 & 2), p. 160.

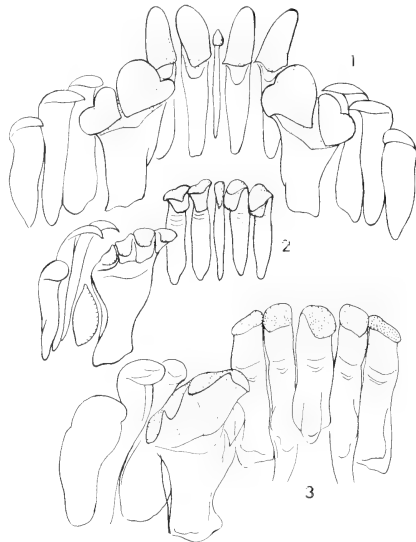


Plate 104. Fig. 1. *Patella (Scutellastra) kermadecensis* Pilsbry, Raoul Island, Kermadec Islands. Radula. Fig. 2. *Patella (Scutellastra) flexuosa* Quoy & Gaimard, Rarotonga, Cook Islands. Radula. Fig. 3. *Patella (Scutellastra) exusta* subspecies *pica* Reeve, Mauritius. Radula.



Plate 105. *Patella (Scutellastra) aurorae* Fleming, 1973. Mason River, North Canterbury, New Zealand. Duntroonian Pligocene.

***Patella tucopiana* (Powell, 1925)**

(Pl. 106)

Range—Tikopia (Tucopia) Island, Melanesia.

Remarks—A large solid limpet, but evidently of smaller adult size than *kermadecensis*, from which it differs in shape, being regularly ovate, not narrowed anteriorly, and also in the coloration of the exterior, which is black instead of orange. The writer knows of only the two type specimens of this rare species. They were obtained from a native of Tikopia who stated that they came from a nearby reef.

Description—Shell large, up to 92 mm. (3½ inches) in length, solid, ovate, depressed, the apex at about the anterior third, anterior slope almost straight, posterior slope convex, margin weakly crenulated. Sculpture consisting of numerous low narrow irregular radial ribs, 10 of them primary, and between 80 and 85 secondary radials. Colour of exterior dull black, more deeply impregnated in the rib interstices; interior creamy-white, with the spatula tinged pale flesh-colour; margin with a narrow amber coloured border, through which the external colour shows as a continuous series of irregular black dashes.

Measurements (mm.)—

length	width	height	
92.0	73.0	25.0	holotype
81.0	63.0	22.0	paratype

Synonymy—

1925 *Scutellastra tucopiana* Powell, Proc. Malac. Soc., London, vol. 16, pt. 4, p. 169.

Types—The holotype and paratype are in the Powell collection, Auckland. Known only from the type locality.

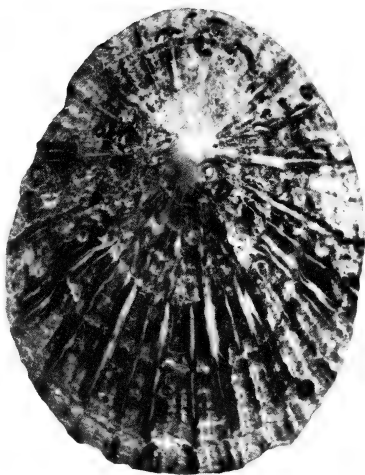


Plate 106. *Patella (Scutellastra) tucopiana* (Powell, 1925). Tikopia Island, Melanesia. Holotype (above), 92 mm., and paratype, 81 mm., AWP coll. 206.

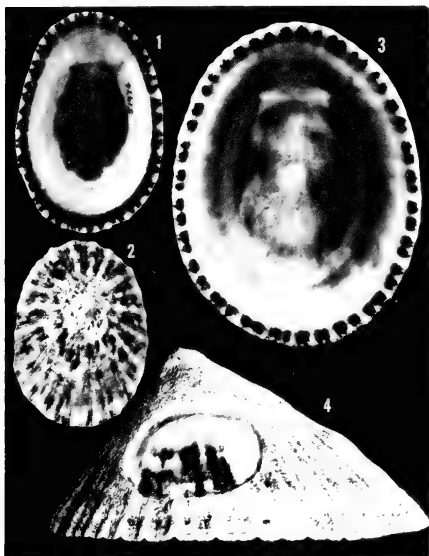


Plate 107. Figs. 1-4. *Patella (Scutellastra) laticostata* Blainville, 1825. Figs. 1, 2. Yellengap, Western Australia, 46-50 mm., AWP coll. 51976. Figs. 3, 4. Cape Naturaliste, Western Australia, 81.5 mm., AWP coll. 29117.

Patella laticostata Blainville, 1825

(Pl. 66, figs. 3, 4; Pls. 107 and 113)

Range—Western South Australia to southern Western Australia; lower littoral zone.

Remarks—This is the largest member of the subgenus *Scutellastra* found in Australian waters.

It is easily recognised by its solidity, large size, often over four inches in length, narrowly-ovate shape and high-conical profile. The interior is creamy-white, varying stained with orange-brown, and there is a marginal border of dark-brown maculations. The exterior is nearly always eroded, but in fresh non-eroded examples there is a coarse radial sculpture of dark-brown ribs.

Description—Shell very large, up to 110 mm. (4½ inches) in length, very solid, narrowly-ovate, and frequently high in profile, the apex at about the anterior third. Radial ribbing coarse and irregular in size; juveniles with about 22 primary ribs, increasing by interpolation to about 50 primaries in the adult, and there are finer subsidiary radials in the interstices. Interior porcellanous, with the crenulated border variably maculated, and with a well-defined, very large spatula, mainly white, or diffused with yellowish brown, but often surrounded at its outer edge by an irregular zone of deep orange-brown. The margin is rather wide in young shells but relatively narrow in the fully adult, and bears numerous radiate lines or thick dashes, in dark-brown, on a whitish ground. Externally the shell is usually eroded to a dull greenish grey, and sometimes bears one or two specimens of the acmaeid, *Patelloida nigrosulcata* (Reeve), which deeply excavate the surface.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. There are five central teeth, the middle one as long as, but narrower than, the other four, each with a single well-developed shovel-shaped cusp; the large palmate lateral bears four blunt cusps, and each of the three, slender, rod-like marginals has a blunt poorly developed cusp (see Macpherson, 1955, p. 235).

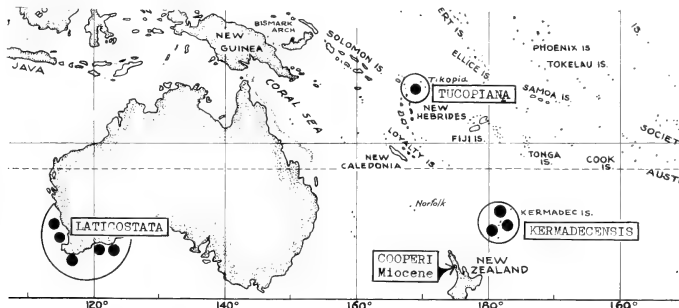


Plate 108. Geographical distribution of *Patella (Scutellastra) laticostata* Blainville, *Patella (Scutellastra) kermadecensis* Pilsbry, *Patella (Scutellastra) tucupiana* (Powell), and the

New Zealand Miocene *Patella (Scutellastra) cooperi* (Powell). These are all large species, comparable in size with the largest of the South African members.

Measurements (mm.).—

length	width	height	
110.0	85.0	54.0	all Charley Island,
92.0	68.0	35.0	Archipelago of the
83.0	60.0	56.0	Recherche
77.0	53.5	29.0	

Synonymy.—

- 1825 *Patella laticostata* Blainville, Dict. Sci. Nat., vol. 38, p. 111.
 1826 *Patella neglecta* Gray, King's Intertropical Survey Aust., vol. 2, pp. 156, 182, 492.
 1843 *Patella rustica* Menke, Moll. New Holl., p. 33.
 1854 *Patella zebra* Reeve, Conch. Iconica, vol. 8, pl. 4, figs. 7a, b. Swan River. (non Blainville)
 1891 *Patella* (*Scutellastra*) *neglecta* Gray, Pilsbry, Man. Conch., vol. 13, p. 95, pl. 20, fig. 41.
 1924 *Patella laticostata* Blainville, Iredale, Proc. Linn. Soc. N.S.W., vol. 49, p. 241.
 1955 *Patellanax laticostata* Blainville, Macpherson, Proc. Roy. Soc. Vict., vol. 67 (2), p. 234, text figs., pl. 8, fig. 4.
 1959 *Cellana laticostata* Blainville, Cotton, S. Aust. Moll., Archaeogast., Govt. Print., Adelaide, p. 292.

Records—Western SOUTH AUSTRALIA: Port Lincoln and Streaky Bay (B. C. Cotton, 1959). South WESTERN AUSTRALIA: King George Sound (B. C. Cotton, 1959); Charley Island, Archipelago of the Recherche; Quarantine Ground, Albany; Foul Bay; Cape Naturaliste; Garden Island, Fremantle (all AWBP coll.). A record from Shark Bay, North Western Australia (B. C. Cotton, 1959) requires confirmation.

***Patella peronii* Blainville, 1825**

(Pl. 65, figs. 11-13; Pls. 109 and 113)

Range—Australia; from southern Western Australia to Victoria, Tasmania and New South Wales.

Remarks—This species, also, is extremely variable in shape and in sculptural development, ranging from typical *peronii*, which is weakly but regularly smooth ribbed, thus producing an almost smooth margin, to the strongly squamose sculptured *squamifera* form, in which the margin becomes noticeably corrugated. Dr. Hope Macpherson (1955) claimed that when large series were examined, both forms were seen to intergrade, and no differences in the radula were apparent. Common on exposed rock platforms of the lower littoral zone to the sublittoral fringe, among holdfasts of giant kelp.

Description—Shell of moderate size, averaging about 35 mm. but reaching 47 mm. (1½ to 1¾ inches) in length, solid, tall-conical, with the apex varying between subcentral and the anterior fourth. Sculpture extremely variable, ranging from low, rounded, primary radials with 4 to 6 radial threads in the interspaces (typical form), to

strongly sculptured shells with about 24 bold carinated and spinose primary radials, with a few relatively strong interstitial radials (*forma squamifera*). Colour, externally yellowish brown with the radials paler, interior porcellaneous-white with a faint yellowish brown spatula. In the typical *peronii* form the secondary radial interspaces are often lined in black. Shell margin thin semitransparent, yellowish with the external interstitial lines showing through. The shell margin varies according to the strength of the external sculpture being almost smooth in the *peronii* form but strongly corrugated in the *squamifera* form.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Central teeth five, the middle one much smaller than the other four, lateral with four cusps, followed by the usual three functionless marginals (Macpherson, 1955, p. 233).

Measurements (mm.).—(A) = typical *peronii*; (B) = *squamifera* form.

length	width	height	
47.0	39.0	24.0	Port Arthur, Tasmania; (A)
43.5	34.0	16.0	Port Jackson; (B)
37.4	29.5	15.0	New South Wales; (B)
31.5	25.0	12.5	Shellharbour, N.S.W.; (B)

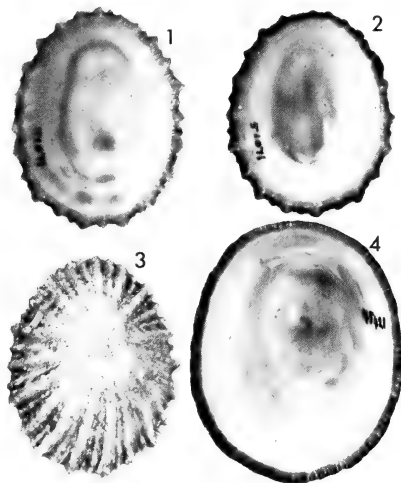


Plate 109. Figs. 1-4. *Patella* (*Scutellastra*) *peronii* Blainville, 1825. Figs. 1, 2. Merimbula, New South Wales, 39-42 mm., AWBP coll. 51071. Fig. 3. Port Jackson, New South Wales, 43 mm., AWBP coll. 212 (*squamifera* form). Fig. 4. Port Arthur, Tasmania, 47 mm., AWBP coll. 45421 (*peronii* = *ustulata* form).

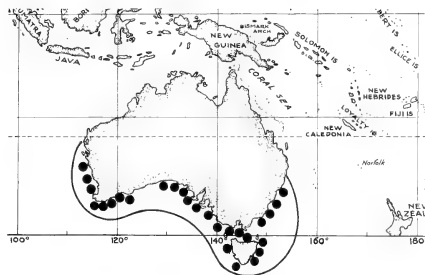


Plate 110. Geographical distribution of *Patella (Scutellastra) peronii* Blainville.

Synonymy—

- 1825 *Patella peronii* Blainville, Dict. Sci. Nat., vol. 38, p. 111.
 1848 *Patella diemenensis* Philippi, Zeitsch. f. Malak., vol. 5, p. 162.
 1855 *Patella ustulata* Reeve, Conch. Iconica, pl. 31, figs. 58a, b.
 1855 *Patella aculeata* Reeve, Conch. Iconica, pl. 32, fig. 90 (non Gmelin).
 1855 *Patella squamifera* Reeve, Conch. Iconica, pl. 32, fig. 94.
 1876 *Patella tasmanica* T. Woods, Proc. Roy. Soc. Tasman., p. 157.
 1891 *Patella (Scutellastra) ustulata* Reeve, Pilsbry, Man. Conch., vol. 13, p. 101, pl. 22, figs. 11, 12.
 1891 *Patella (Scutellastra) aculeata* Reeve, Pilsbry, Man. Conch., vol. 13, p. 100, pl. 25, figs. 20, 21; pl. 62, figs. 11, 12.
 1906 *Patella hepatica*, Verco, Trans. Roy. Soc. S. Aust., vol. 30, p. 207. Non P. and G.
 1924 *Patellanax squamifera* Reeve, Iredale, Proc. Linn. Soc. N. S. W., vol. 49, p. 239.
 1955 *Patellanax peroni* Blainville, Macpherson, Proc. Roy. Soc. Vict., vol. 67, pt. 2, pp. 232, 233, text figs. (shells and radula).
 1957 *Patellanax peronii* Blainville, Cotton, South. Aust. Moll. Archaeogast., Govt. Print., Adelaide, p. 290, text fig. 194.

Records—Southern WESTERN AUSTRALIA: King George Sound (type locality). SOUTH AUSTRALIA: Marino, VICTORIA: near Port Phillip Heads. TASMANIA: Port Arthur; Blackman's Bay. NEW SOUTH WALES: Merimbula; Port Jackson; Cronulla; Shellharbour (all AWP coll.).

Patella chapmani Tenison-Woods, 1875

(Pl. 111; Pl. 113, fig. 3)

Range—Southern half of Australia and Tasmania.

Remarks—This is a small white limpet that assumes different outlines, varying from irregularly-lobed to a regular 8-pointed star. This latter form, more common in New South Wales is the "*Acmaea saccharina* var. *perplexa*" of Pilsbry, 1891. It lives in the lower littoral zone among algae on rock platforms and boulders.

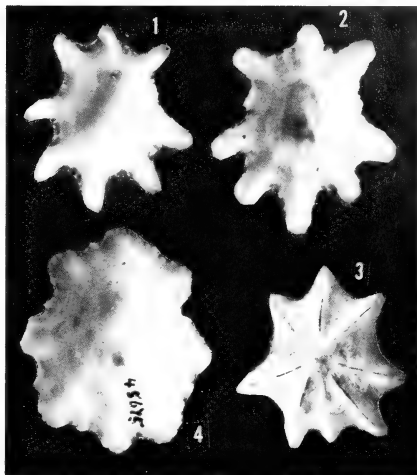


Plate 111. Figs. 1-4. *Patella (Scutellastra) chapmani* Tenison Woods, 1875. Figs. 1-3. Kurnell Botany Bay, New South Wales, 22.5-25 mm., AWP coll. 19573. Fig. 4. North Harbour, Port Jackson, New South Wales, 31 mm., AWP coll. 45675.

Description—Shell small, average length 20 mm. (% of an inch) but grows up to 30 mm. (1½ inches), irregularly to regularly star-shaped, with eight prominent radial ribs that project to a varying extent; irregularly and weakly lobate in typical *chapmani*, regularly and strongly projecting and narrowly-pointed in the form *perplexa*. Surface sculptured with numerous radial, weakly-scabrous lirae, the centre one down each of the eight radial folds being stronger than the rest. Colour of exterior buff, with scattered flecks of light-brown, and often, especially in the *perplexa* form, with a narrow reddish brown line down the crest of each of the eight radial folds. Interior porcellaneous-white, without a clearly defined spatula.

Radula—Formula 3 + 1 + (2+1+2) + 1 + 3. Central teeth five, the middle one only half the size of the other four, lateral massive with four cusps, and the three marginals long and slender, each with a weak blunt cusp.

Measurements (mm.)—

length	width	height	
30.0	28.0	12.0	North Harbour, Sydney
28.5	27.0	6.0	Kurnell, N. S. W.
23.0	19.5	6.0	Kurnell, N. S. W.
18.5	16.0	4.0	Kurnell, N. S. W.

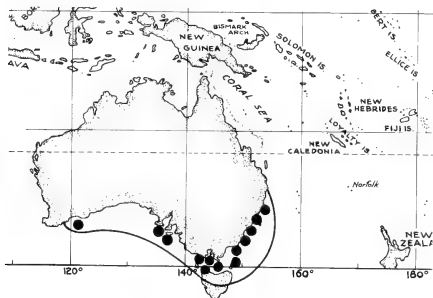


Plate 112. Geographical distribution of *Patella (Scutellastra) chapmani* Tenison Woods.

Synonymy—

- 1873 *Patella octoradiata* Hutton, Cat. Mar. Moll. N. Z., p. 44 (erroneously attributed to New Zealand). (non Gmelin).
 1875 *Patella chapmani* Tenison-Woods, Proc. Roy. Soc. Tas., p. 157.
 1876 *Acmaea alba* Tenison-Woods, Proc. Roy. Soc. Tas., p. 155.
 1891 *Acmaea saccharina perplexa* Pilsbry, Man. Conch., vol. 13, p. 50, pl. 36, figs. 69, 71.
 1915 *Patelloida perplexa* Pilsbry, Iredale, Trans. N. Z. Inst., vol. 47, p. 430.
 1922 *Patella perplexa* Pilsbry, Peile, Proc. Malac. Soc., Lond., vol. 15, p. 16, text fig. 4.
 1924 *Patella perplexa* Pilsbry, Iredale, Proc. Linn. Soc. N. S. W., vol. 49, p. 238.
 1924 *Scutellastra chapmani* Tenison-Woods, Oliver, N. Z. J. Sci. Tech., vol. 7, p. 244 (radula).
 1955 *Patellanax chapmani* Tenison-Woods, Macpherson, Proc. Roy. Soc. Vict., vol. 67, pt. 2, p. 231, text figs.; pl. 8, figs. 1, 2.
 1959 *Patellanax alba* Tenison-Woods, Cotton, S. Aust. Moll., Archaeogast., Govt. Print., Adelaide, p. 258.

Types—The types of *chapmani* and of *alba* are in the Tasmanian Museum, Hobart, and that of *perplexa* in the Academy of Natural Sciences of Philadelphia.

Records—AUSTRALIA: NEW SOUTH WALES; Angourie, north coast; North Harbour, Port Jackson; Kurnell, Botany Bay; Shellharbour; TASMANIA (type locality of *chapmani*); (all AWBP coll.). SOUTH AUSTRALIA: VICTORIA and southern WESTERN AUSTRALIA (Cotton, 1959).

Patella hamiltonensis (Chapman and Gabriel, 1923)

Range—Muddy Creek, upper beds, Victoria, Australia, Kalimnan, lower Pliocene.

Remarks—This species, described as an acmaeid, and compared with "*Patelloida perplexa* Pilsbry" by its authors, was recently referred to *Patellanax* by Darragh, 1970. The present writer has not seen the type material but accepts Darragh's location

of the species in the Patellidae. The original description follows, but the original accompanying illustration is not clear enough for copying.

Description—"Shell solid, irregularly oval, strongly ribbed; apex sub-central, much eroded and probably originally smooth. The sculpture consisting of about ten rather prominent radiating ribs, the interspaces of which are occupied by finer riblets of varying strength. About three, irregular growth stages are discernible on the shell surface, which are marked by slight overlapping or sulcation. The area between the major ribs, depressed or fluted, resulting in an undulose margin to the shell. Colour pale ochre."

Observations—This species approaches *Patelloida perplexa* Pilsbry, but differs in the ribs being less pronounced and not salient at the margins." [Acmaea saccharina var. *perplexa* Pilsbry, 1891, is actually a synonym of *Patella (Scutellastra) chapmani* Tenison-Woods, 1875].

Measurements (mm.)—

length	width	height
13.0	12.0	5.5 holotype

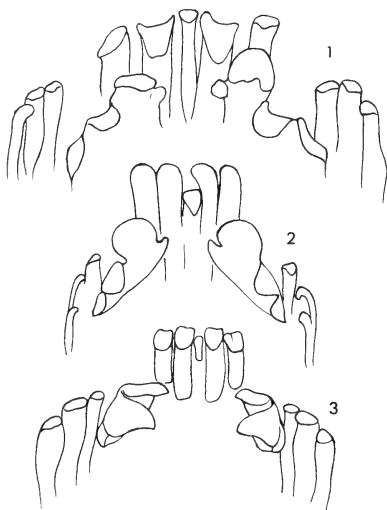


Plate 113. Fig. 1. *Patella (Scutellastra) laticostata* Blainville, southern Western Australia. Radula, from Macpherson, 1955, p. 235, text fig. Fig. 2. *Patella (Scutellastra) peronii* Blainville, Victoria. Radula, from Macpherson, 1955, p. 233, text fig. Fig. 3. *Patella (Scutellastra) chapmani* Tenison Woods (as *P. perplexa* Pilsbry), New South Wales. Radula, from Peile, 1922, Proc. Malac. Soc., vol. 15, p. 16, fig. 4.

Synonymy—

- 1923 *Patelloida hamiltonensis* Chapman & Gabriel, Proc. Roy. Soc. Victoria, vol. 36 (N. S.), pt. 1, p. 24, pl. 1, fig. 3.
 1970 *Patellanax hamiltonensis*: Darragh, Mem. National Mus. Victoria, vol. 31, p. 173.

Types—The holotype and two paratypes are in the National Museum of Victoria, Melbourne, Australia.

***Patella cooperi* (Powell, 1938)**

(Pl. 114)

Range—New Zealand, lower Miocene.

Remarks—The species belongs to the wide ranging Indo-Pacific *flexuosa* group, but just how closely related is this Miocene species, cannot be determined on the basis of the only known examples, both of which are in an eroded and badly damaged condition.

Description—Shell of moderate size, 50 mm. (2 inches) or more in length, solid, depressed, elongated, star-shaped, with eight principal radial ribs that are carinated, very prominent, and strongly projecting at the margin. In the interstices there are from 3 to 5 secondary ribs. Apex estimated at about the anterior third.

Measurements (mm.)—

length	width	height
50.0	38.0	9.0 (approximately); holotype

Synonymy—

- 1938 *Scutellastra cooperi* Powell, Trans. Royal Soc. N. Z., vol. 68, p. 379, pl. 39, figs. 13, 14.

Records—NEW ZEALAND: Motuihi Island, south coast, Auckland, in conglomerate, basal Waitemata Group, Otaian Stage, lower Miocene.

Types—Holotype and paratype in the Auckland Museum.



Plate 114. *Patella (Scutellastra) cooperi* (Powell, 1938), New Zealand, Motuihi Island, Auckland, Otaian, lower Miocene. Fig. 1. Holotype, 50 mm., Auck. Mus. 706. Fig. 2. Paratype, 69 mm., Auck. Mus.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus ANCISTROMESUS Dall, 1871

Type: *Patella mexicana* Broderip and Sowerby, 1829

This is the largest known patellid limpet which sometimes attains a length of 14 inches. It is the only known true patellid living on the west coast of the Americas, with the exception of the subantarctic *Nacella* and *Patinigera*, of which the latter extends up the Chilean coast as far north as Valparaiso.

Dall's subgenus is based largely upon the different form of the branchial lamellae, which are not semicircular as in other patellids, but are produced, twisted and elongated, having an arborescent appearance. Also, unique among patellids, the entire animal is black, more or less marbled and streaked with white.

The radula is similar to that of other Indo-Pacific *Patella* except that the median central tooth is fully developed so that there are five evenly-developed centrals in one horizontal series. In other Indo-Pacific *Patella* species the median central tooth is much smaller, vestigial, or occasionally absent, as it is in the European *Patella vulgata*.

Undoubtedly there is some relationship between *Ancistromes* and large Indo-Pacific patellids, such as *kermadecensis* Pilsbry and *tucopiana*

Powell. It is assumed that *Ancistromes* owes its presence in the tropical West American fauna, as an extreme Indo-Pacific outlier, having reached there in the geological past when the ancient Tethys Sea offered a free equatorial water-way around the globe.

Synonymy—

1871 *Ancistromes* Dall, American Journal of Conchology, vol. 6, part 3, p. 266. Type, by monotypy, *Patella mexicana* Broderip and Sowerby, 1829.

Patella mexicana Broderip and Sowerby, 1829

(Pl. 115)

Range—Gulf of California to Peru.

Remarks—Apart from its solidity and huge adult size, *mexicana* has a consistently narrowly ovate outline, and young shells are at once recognised by the presence of a broad, thin, semitransparent margin that extends out abruptly from the outer edge of the porcellaneous interior.

It is almost certain that *Patella gigantea* Lesson, 1831, described from a shell "thrown on the coral rocks" at Borabora, Society Islands, is a *mexicana* that was probably taken there and discarded by a sailor from one of the many whalers that frequented the area at about the time. Apparently Lesson's shell has never been figured, and enquiries concerning the existence or not of the type specimen were abortive, since at the time of writing, the molluscan collections of the Museum National d' Histoire Naturelle, Paris, were under general reorganisation.

Dr. Harald A. Rehder of the National Museum

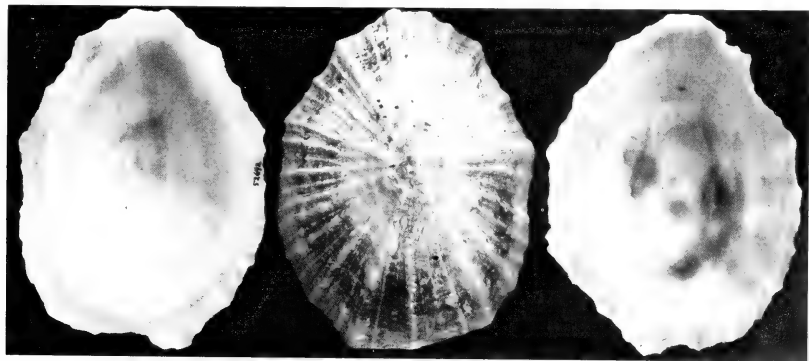


Plate 115. *Patella (Ancistromes) mexicana* Broderip & Sowerby, 1829. Mazatlan, West Mexico, 107-116 mm. AWBP

coll. 52692. The world's largest limpet, known to attain a length of 355 mm. - 14 inches.

of Natural History, Washington, who has just spent six months of intensive collecting at Borabora and neighbouring areas, did not find any large limpets resembling *gigantea*, and he also is of the opinion that *gigantea* should be considered a synonym of *mexicana* (personal communication).

The dimensions given by Lesson for his *gigantea*, the equivalent of 7 by 5 inches, match exactly the length-width ratio of a series of *mexicana*. Also Lesson's description of the interior of his shell—"L' intérieur est lisse, blanchâtre, avec le fond rougeâtre", applies to occasional examples of *mexicana*, the reddish brown staining of the spatula area, occurring when the outer surface has been extensively eroded.

Description—Shell massive and very large, 200 to 355 mm. (8 to 14 inches) in length, depressed in its younger stages but moderately elevated in the adult, with the apex subcentral to a little nearer to the anterior end. Outline elongate-ovate, noticeably narrowed at the anterior end, the margin thin, wide, flattened and irregularly corrugated in juveniles, but thickened and minutely crenulated in the adult. Sculpture in young shells consisting of eleven low and broad primary radials and a varying number of secondary radials in between. Adult shells are almost invariably eroded, encrusted, or riddled by boring bivalves. Colour dull-white externally and porcellaneous-white within, sometimes diffused with reddish brown over the spatula. In young shells the broad flat thin margin is semitransparent.

Measurements (mm.)—

length	width	height	
355.0	—	—	Keen, 1958, p. 242
185.0	148.0	ca 60.0	Caleta, Acapulco
158.0	114.0	67.0	Caleta, Acapulco
95.0	75.0	16.0	Acapulco

Synonymy—

- 1829 *Patella mexicana* Broderip and Sowerby, Zool. Journ., vol. 4, p. 369.
 1831 *Patella gigantea* Lesson, Voy. Coquille, Zool., vol. 2, p. 423.
 1841 *Patella maxima* Orbigny, Moll. Amér. Mérid., p. 482.
 1855 *Patella mexicana* Brod. and Sby., Reeve, Conch. Iconica, pl. 1, fig. 1.
 1871 *Ancistromesus mexicanus* Brod. and Sby., Dall, Amer. Journ. Conch., vol. 6, pt. 3.
 1891 *Patella gigantea* Lesson, Pilsbry, Man. Conch., vol. 13, p. 156.
 1891 *Patella mexicana* Brod. and Sby., Pilsbry, Man. Conch., vol. 13, p. 108, pl. 31, figs. 59-62.
 1958 *Patella (Ancistromesus) mexicana* Brod. and Sby., Keen, Seashells Trop. W. America, p. 242.

***Patella fuenzalidai* Herm, 1969**

(Pl. 116)

Range—Pliocene of northern Caldera Province, Atacama, North Chile.

Remarks—This species differs from the Recent *mexicana* in being more broadly ovate, much finer sculptured, with the primary radials almost obsolete, and in having a much narrower margining bevel.

Description—Shell massive and very large, 188-209 mm. (7½-8¼ inches) in length, broadly ovate, only slightly narrowed towards the anterior end, and rather elevated. Sculpture very densely and finely radially liriate, and obsoletely eight-rayed, the rays visible only by the flattened planes between them. Apex a little anterior to the middle. Interior with a large well defined spatula, and a relatively narrow bevelled margin at the perimeter of the shell.

Measurements (mm.)—

length	width	height	
209.0	187.0	68.0	holotype
188.0	161.0	61.0	paratype

Synonymy—

1969 *Patella (Ancistromesus) fuenzalidai* Herm, Zitteliana, vol. 2, p. 131, pl. 14, figs. 1-3.

Types—The location of the type is unknown to us.

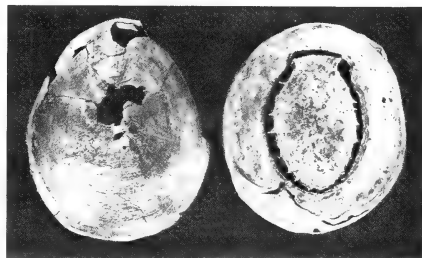


Plate 116. *Patella (Ancistromesus) fuenzalidai* Herm, 1969. South America, northern Caldera Province, Atacama, North Chile, Pliocene. Holotype, 209 mm., and paratype, 188 mm., from Herm, 1969, Zitteliana, 2, pl. 14, figs. 1, 2.

Genus *Helcion* Montfort, 1810

Type: *Helcion pectunculus* (Gmelin, 1791)

This genus has a radula identical with that of *Patella*, but the gill cordon, unlike that of *Patella*, is interrupted in front by the head as it is in *Cellana*. The radula in *Cellana* differs from that of both the above genera in consisting of a pair of central teeth followed by a pair of laterals. The shell of typical *Helcion* is cap-shaped, high-arched, with the incurved apex almost at the anterior end. The sculpture consists of radial scaly ribs.

Synonymy—

1810 *Helcion* Montfort, Conchyliologie Systématique et Classification Méthodique des Coquilles, vol. 2, pp. 62, 63. Type, by monotypy: *Helcion pectinatus* Montfort, 1810, which is *Patella pectunculus* Gmelin, 1791.

Helcion pectunculus (Gmelin, 1791)

(Pl. 117, figs. 1, 2; Pl. 118, fig. 1)

Range—South Africa.

Remarks—This is a common intertidal species.

Description—Shell rather small, up to 28 mm. (over 1 inch) in length, solid, roundly ovate, high arched, with the apex incurved and almost at the anterior end. Sculptured with numerous scaly to spinose ribs, both primary and secondary. Colour buff to light brownish with the ribs black; interior varying from dull leaden to orange-brown. Often the black radials are interrupted, resulting in a tessellated pattern.

Measurements (mm.)—

length	width	height	
28.0	24.0	13.0	Port Elizabeth
23.5	19.5	9.0	Port Elizabeth

Synonymy—

1778 *Patella pectinata* Linn., Born, Index Rerum Natur. Mus. Caes. Vind., p. 441.

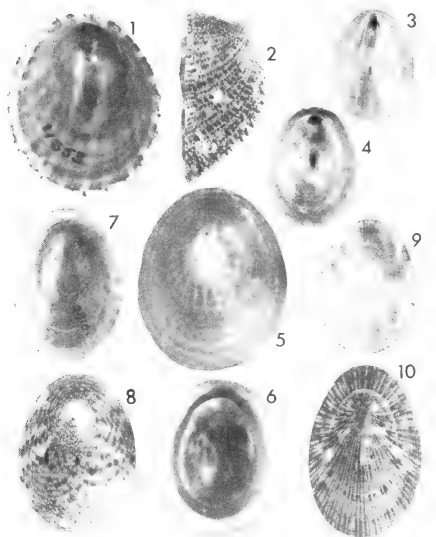


Plate 117. Figs. 1, 2. *Helcion pectunculus* (Gmelin, 1791). Port Elizabeth, South Africa, 28 mm., AWBP coll. 11853. Figs. 3-6. *Helcion (Ansates) pellucidus* (Linnaeus, 1758). Figs. 3, 4. South coast, England, 14 mm., Auck. Mus. 19409. Figs. 5, 6. (*laevis* form), 20-24 mm., south coast England, AWBP coll. 52497. Figs. 7, 8. *Helcion (Patinastra) pruinosis* (Krauss, 1848). Algoa Bay, South Africa, 23-25 mm., AWBP coll. 2910. Figs. 9, 10. *Helcion (Patinastra) dunkeri* (Krauss, 1848). Port Alfred, South Africa, 15-20 mm., AWBP coll. 52495.

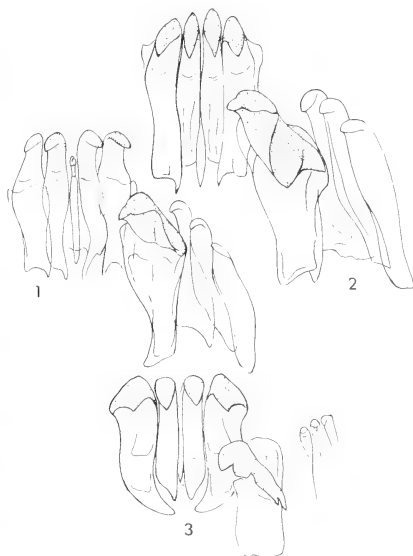


Plate 118. Fig. 1. *Helcion pectunculus* (Gmelin), "Red Sea", in error ~ South Africa. Radula, from Thiele, 1891, pl. 28, fig. 23. Fig. 2. *Helcion (Patinastra) pruinosis* (Krauss), Cape of Good Hope. Radula, from Thiele, 1891, pl. 28, fig. 24. Fig. 3. *Helcion (Ansates) pellucidus* (Linnaeus), Heligoland. Radula, from Thiele, 1891, pl. 28, fig. 26.

- 1780 *Patella pectinata* Born. Test. Mus. Caes. Vind., p. 423, pl. 18, fig. 7. (non Linnaeus, 1758).
 1791 *Patella pectunculus* Gmelin, Syst. Nat. ed. 13, p. 3713; based upon Martini-Chemnitz, Conch. Cab., vol. 1, pl. 7, figs. 56, 57.
 1810 *Helcion pectinatus* Montfort, Conchyl. Systém., vol. 2, p. 62.
 1845 *Patella pectinata* Linne', Krauss, Südafr. Moll., Stuttgart, p. 57.
 1891 *Patella (Helcion) pectinata* Linn. Pilsbry, Man. Conch., vol. 13, p. 109, pl. 51, figs. 1-3.
 1891 *Helcion pectunculus* Gmelin, Troschel and Thiele, Das Gebiss der Schnecken, vol. 2, pl. 28, fig. 23 (radula).
 1948 *Helcion pectunculus* Gmelin, Stephenson, Ann. Natal. Mus., vol. 11, part 2, p. 278, text fig. 10 (radula).

Records—SOUTH AFRICA: Cape of Good Hope (AWBP coll.); Port Elizabeth (AWBP coll.); Port Natal (AWBP coll.); Gouritz River mouth, Cape Province (V. Orr, 1955; Auck. Mus.); Durban (Auck. Mus.).

Subgenus ANSATES Sowerby, 1839

Type: Patella pellucida Linnaeus, 1758

This subgenus differs from typical *Helcion* in being almost smooth. The type species is a seaweed dweller, which accounts for its comparatively light build and weak sculpture.

Synonymy—

- 1839 *Ansates* Sowerby, Conchological Manual, p. 6. Type, by monotypy: *Patella pellucida* Linnaeus, 1758.
 1847 *Patina* Gray, Synopsis of Contents of British Museum ed. 42, p. 148 (non Rafinesque, 1815).

Helcion pellucidus (Linnaeus, 1758)

(Pl. 117, figs. 3-6; Pl. 118, fig. 3)

Range—Seas of western Europe, from Lofoten Islands, Norway, to Portugal.

Remarks—The typical form of this attractive little cap-shaped shell is smooth, and of orange-brown colour, with a few sky-blue longitudinal lines. It lives on *Laminaria* and *Fucus* seaweeds, to a depth of about 15 fathoms. The variety *laevis* is a gerontic form of the species that is thicker, larger, and flattens out towards the

margin, where the sculpture is more pronounced. Such shells are always ledged, the early portion being exactly like normal *pellucidus*. Pilsbry (1891) remarked that the *laevis* variety is due to station, such individuals being found partly embedded in the stems of *Fucus*.

Description—Shell small, up to 24 mm. (1 inch) in length, usually rather thin, ovate, high-arched, the apex immersed and situated towards the anterior end. Surface smooth and polished, with very weak radial riblets. Colour golden brown, black tipped at the apex, and usually with a few vivid sky-blue lines running back from the apex to the posterior margin.

Measurements (mm.)—

length	width	height	
24.0	20.3	10.0	England; <i>laevis</i> form
20.0	15.0	8.0	Pilsbry, 1891, p. 110
14.0	11.0	5.0	S. coast, England

Synonymy—

- 1758 *Patella pellucida* Linnaeus, Syst. Nat., ed. 10, p. 783.
 1777 *Patella laevis* Pennant, Brit. Zool., ed. 4, vol. 4, p. 125.
 1777 *Patella intorta* Pennant, Brit. Zool., ed. 4, vol. 4, p. 125.
 1778 *Patella coeruleata* da Costa, Brit. Conch., p. 7, pl. 1, figs. 5, 6.
 1779 *Patella cornea* Helbling, Abh. Privatges. Bohm., vol. 4, p. 107.
 1803 *Patella bimaculata* Montagu, Test. Brit., vol. 2, p. 482.
 1811 *Patella cypridium* Perry, Conchology, London, pl. 43, fig. 6.
 1813 *Patella elongata* Fleming, Brewster's Edinb. Encycl., vol. 7 (1), p. 65.
 1813 *Patella elliptica* Fleming, Brewster's Edinb. Encycl., vol. 7 (1), p. 65.
 1838 *Patella cornea* Potiez & Michaud, Gal. Moll. Douai, vol. 1, p. 525.
 1891 *Helcion (Patina) pellucida* L., Pilsbry, Man. Conch., vol. 13, p. 110, pl. 51, figs. 4-10.
 1891 *Patina pellucida* Linn., Thiele, in Troschel & Thiele, Das Gebiss der Schnecken, vol. 2, pl. 28, fig. 26 (radula).

Radula—Formula 3 + 1 + (4) + 1 + 3, very similar to the radula of *Patella* except that the two outer centrals are larger than the inner two; there is no trace of a median central.

? *Helcion tella* (Bergh, 1871)

Range—Sargasso Sea

Remarks—This species was described from the soft parts only, of a poorly preserved specimen, the shell of which had been detached and lost. Its author compared his species with the European *Helcion (Ansates) pellucidus* (Linnaeus).

Synonymy—

- 1871 *Patina tella* Bergh, Verhandl. der k.-k. zool. bot. Gesellsch., Wien, 21, p. 1297.
 1891 *Patina tella* Bergh, Pilsbry, Man. Conch., 13, pp. 111-112.

Subgenus PATINASTRA Thiele in Troschel, 1891Type: *Helcion (Patinastrea) pruinusos* (Krauss, 1848)

Shell very similar to that of *Cellana*, being low and spreading with the apex varying between the anterior fourth and fifth, but the gill cordon is complete as in *Patella*. Radula similar to that of *Ansates*, except for the marginals which are very large. Recent, South Africa.

Synonymy—

1891 *Patinastrea* Thiele in Troschel, Das Gebiss der Schnecken, vol. 2, p. 325. Type, by monotypy: *Patella pruinosa* Krauss, 1848.

Helcion pruinusos (Krauss, 1848)

(Pl. 117, figs. 7, 8; Pl. 118, fig. 3)

Range—South Africa, generally distributed.

Remarks—A thin oval shell of low profile, yellowish-olive, variously rayed and speckled in dark green or brown, easily distinguished from the next species, *dunkeri*, by its almost smooth surface and radial series of sky-blue spots.

Description—Shell rather small, up to 31 mm. (1¼ inches) in length, but usually about 23 mm. (¾ of an inch), rather thin, elongate ovate, narrowed anteriorly, rather depressed, and with the apex at about the anterior fifth. Sculpture weak, consisting of very numerous narrow radial thread crossed by dense, much finer, concentric lirae. Colour of exterior yellowish olive sparingly dark-brown speckled and with most of the radials minutely dotted with sky-blue. Interior yellowish olive, shining, without a clearly defined spatula.

Measurements (mm.)—

length	width	height	
31.0	24.0	9.0	Pilsbry, 1891, p. 113
24.3	19.0	6.0	Algoa Bay
22.0	17.0	5.0	Algoa Bay

Synonymy—

- 1848 *Patella pruinosa* Krauss, Südaf. Moll., Stuttgart, p. 56, pl. 3, fig. 9.
 1855 *Patella pruinosa* Krauss, Reeve, Conch. Iconica, pl. 35, figs. 109 a, b.
 1891 *Patinastrea pruinosa* Krauss, Thiele in Troschel and Thiele, Das Gebiss der Schnecken, vol. 2, p. 325, pl. 28, fig. 24 (radula).
 1891 *Helcion (Patinastrea) pruinosa* Krauss, Pilsbry, Man. Conch., vol. 13, p. 113, pl. 51, fig. 11; pl. 13, figs. 68, 69.

1931 *Patella pruinosa fuscocoriadate* Turton, Mar. Shells Port Alfred, p. 171, pl. 40, fig. 1216.

1932 *Patella dunkeri approximata* Turton, Mar. Shells Port Alfred, p. 170, sp. 1210.

1948 *Helcion pruinosa* Krauss, Stephenson, Ann. Nat. Mus., vol. 11, pt. 2, p. 278, text fig. 10 (radula).

Records—SOUTH AFRICA: Cape of Good Hope (type locality); Cape Peninsula (AWBP coll.); Port Alfred (Turton, 1932).

Helcion dunkeri (Krauss, 1848)

(Pl. 117, figs. 9, 10)

Range—South Africa, Natal.

Remarks—A thin oval shell, smaller than *pruinusos*, and differing from that species in being strongly radially ribbed and variously rayed with pink, red, or green but never with sky-blue spots.

Description—Shell small, up to 19.5 mm. (¾ of an inch) in length, very thin, subpellucid, ovate, narrowed anteriorly and rather depressed. Sculpture consisting of very numerous fine radiating lirae, with linear interspaces, the whole crossed by finer and more dense concentric threads. Colour variable, pinkish-white or pale green, radiately lined in pink, red or greenish-brown. Interior shining with the external pattern showing through; spatula indistinct, yellowish to greenish.

Measurements (mm.)—

length	width	height	
19.5	13.0	6.75	Port Alfred
17.0	11.0	4.6	Pilsbry, 1891, p. 148
15.0	11.0	4.0	Port Alfred

Synonymy—

- 1848 *Patella dunkeri* Krauss, Südaf. Moll., Stuttgart, p. 55, pl. 3, fig. 14.
 1855 *Patella dunkeri* Krauss, Reeve, Conch. Iconica, pl. 38, figs. 124 a, b.
 1891 *Helcioniscus dunkeri* Krauss, Pilsbry, Man. Conch., vol. 13, pl. 16, figs. 11-14.
 1932 *Patella conspicua* Philippi, Turton, Mar. Shells Port Alfred, p. 168, sp. 1196 (in part).
 1932 *Patella dunkeri formosa* Turton, Mar. Shells Port Alfred, p. 170, pl. 40, fig. 1211.
 1932 *Patella testudinaria* Linn., Turton, Mar. Shells Port Alfred, p. 170, sp. 1212.
 1932 *Patella rufanensis* Turton, Mar. Shells Port Alfred, p. 171, pl. 40, fig. 1213.
 1932 *Patella gemmula* Turton, Mar. Shells Port Alfred, p. 171, pl. 40, fig. 1214.
 1942 *Helcion dunkeri* Krauss, Tomlin and Stephenson, Proc. Malac. Soc., Lond., vol. 25, pt. 1, pp. 7, 8.
 1948 *Helcion dunkeri* Krauss, Stephenson, Ann. Nat. Mus., vol. 11, pt. 2, p. 278, text fig. 10 (radula).

Records—SOUTH AFRICA: NATAL: Wahlberg (Krauss, 1848; type locality); Port Alfred (AWBP coll.).

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subfamily Nacellinae Thiele, 1929

This subfamily comprises *Cellana* and *Nacella*, with its subgenus *Patinigera*. The chief diagnostic character is in the radula. In the Patelinae it is relatively short and folded back upon itself, but in *Cellana*, and in some species of *Nacella* (*Patinigera*), it is very long, sometimes five times the length of the shell, and coiled in a spiral of several loops. In both *Nacella* and *Cellana* the form and arrangement of the teeth is markedly different from that of *Patella*. In *Patella* there are 4 or 5 central teeth, the median one being absent, vestigial or fully developed. The lateral is large with several prominent cusps, and the three marginals are slender, weakly-cusped and probably functionless. On the other hand, in *Cellana* there is a pair of closely-spaced, long, narrow centrals, alternating with a widely-spaced pair of similar laterals. Between the paired centrals there is a vestigial median plate. The three marginals are as in *Patella*. Both the centrals and the marginals rise vertically almost at right angles to their respective bases.

The gill cordon is interrupted by the head in *Cellana*, but is continuous in *Nacella* and its subgenus *Patinigera*. One feature, the epipodial fringe, is present only in *Nacella* and *Patinigera*.

The shell in the Nacellinae tends towards semi-translucence, is usually highly glazed to iridescent within in *Cellana*, but in *Nacella* (*Patinigera*), it has a bronzy internal lustre.

The genus *Cellana* is restricted to the Indo-Pacific, except in the New Zealand area, where relict populations extend down into the subantarctic. On the other hand *Nacella* and its subgenus *Patinigera* are exclusively cold water inhabitants of Antarctic and Subantarctic waters.

Genus *Cellana* H. Adams, 1869

Type: *Cellana cernica* (H. Adams, 1869)

Shell of similar shape to that of *Patella* but the interior is usually highly glazed and iridescent. The radula differs markedly from that of *Patella* but is very similar to that of *Nacella*. It consists of long recurved pairs of centrals, alternating with similarly-shaped pairs of laterals, usually with an incipient or vestigial median functionless central plate. The three marginals are very weak and functionless also. The whole radula is very

much longer than in *Patella*, sometimes five times the length of the body when straightened out. It lies to the right side of the body where it forms a spiral of up to four double coils.

A feature of the animal is the discontinuity of the gill cordon, which is interrupted by the head, unlike both *Patella* and *Nacella* in which the gill cordon is complete.

The genus is mainly confined to and widely distributed in the Indo-Pacific, ranging from Natal up the east coast of Africa to the Persian Gulf and Arabian Sea, then eastward along the Asiatic coasts to as far north as Japan, the islands of the Indian and Pacific Oceans to the Hawaiian Islands, Society Islands, Juan Fernandez, off the coast of Chile, Australia and New Zealand, including its subantarctic islands to as far south as Campbell Island.

Authentic fossil records for *Cellana* date back to the lower Miocene of both Australia and New Zealand, and *carpentariae* from the Northern Territory of Australia, which looks very like a *Cellana*, could extend the genus back to the lower Cretaceous.

Synonymy—

- 1869 *Cellana* H. Adams, Proceedings of the Zoological Society, London, p. 273. Type, by monotypy: *Nacella* (*Cellana*) *cernica* H. Adams, 1869.
1871 *Helconiscus* Dall, American Journal of Conchology, vol. 6, part 3, p. 277. Type, by original designation: *Patella variegata* Reeve, 1842, which is *Patella capensis* Gmelin, 1791.

Cellana eucosmia (Pilsbry, 1891)

(Pl. 119)

Range—Red Sea and Gulf of Aqaba.

Remarks—This species belongs to the radiata series, but is nearer in shape to *karachiensis* than it is to typical *radiata*. From *karachiensis* it differs in sculpture, being finely radially ribbed, with about every fourth primary a trifle larger, and in

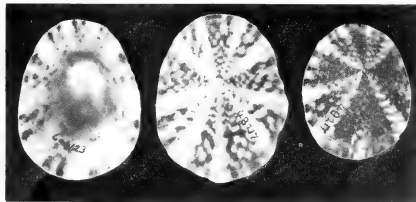


Plate 119. *Cellana eucosmia* Pilsbry, 1891. Ras Banas, Red Sea, 35.5—44.0 mm., AWBP coll. 48217.

its coloration of white flecks and dark maculations in the interstices of a nine-pointed star, the rays of which extend to the margin.

This is Reeve's 1854 version of his *variegata* of 1842, a very different shell, from unknown locality, but here considered to be a synonym of *radiata capensis*. The name *variegata*, however, is not acceptable as of Reeve at either presentation, since there are two prior usages of that name in *Patella*, one of Röding, 1798, and the other of Blainville, 1825.

Dall (1870) correctly localised Reeve's 1854 *variegata* as coming from the Red Sea area, not Australia, as claimed by Reeve. Then in 1891, Pilsbry provided a new name, *eucosmia*, for the *variegata* of Reeve, 1854, and cited the following localities for it—"Suez, Red Sea and Gulf of 'Akaba," Japan and Australia." However, in 1895, in the Stearns "Catalogue of the Marine Mollusca of Japan," pp. 112, 113, Pilsbry, without reasons, switched his *eucosmia* to cover a very different, common Japanese *Cellana*, even adding that "The species is not known from any locality outside of Japan." Pilsbry's 1891 original proposition must stand for the name of the Red Sea *Cellana*, since it was clearly introduced as a new name for the 1854 *variegata* of Reeve, bourn out also by the description, based upon Reeve's 1854 figures.

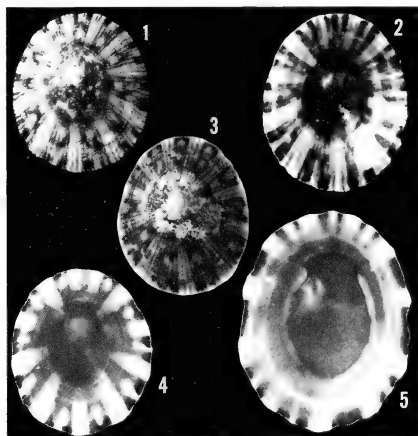


Plate 120. Figs. 1-5. *Cellana radiata* (Born, 1778). Fig. 1. Mt. Lavinia, Ceylon, 22 mm., AWBP coll. 48269. Figs. 2, 3. Colombo, Ceylon, 25-29 mm., AWBP coll. 224978. Fig. 4. Gignoto, Catanduanes Island, Philippines, 23 mm., AWBP coll. 223090. Fig. 5. Fitzroy Island, Queensland, 25.5 mm., (*petalata* form), AWBP coll. 45526.

Description—Shell rather large for the *radiata* group, up to 45 mm. (1¾ inches) in length, ovate, slightly narrowed anteriorly, and of rather low profile, the apex at a little anterior to the middle; anterior slope straight, posterior slope arched. Sculpture consisting of very numerous narrow radial ribs, weakly but densely scaly where crossed by fine concentric lamellae and growth lines. The radials are fairly even, except that about every fourth one is a trifle larger. Colour of exterior pale yellowish brown, with white flecks and dark-brown maculations in the interstices of a pale-brown, nine-pointed star pattern. Interior yellow, with the dark-brown maculations showing through, except for the spatula, which is dark chestnut-brown, usually more or less clouded with white callus.

Measurements (mm.)—

length	width	height	
44.0	35.0	12.0	Ras Banas, Red Sea
40.0	31.0	11.0	Ras Banas, Red Sea
35.5	28.5	12.5	Ras Banas, Red Sea
30.0	24.0	9.0	Berbera, Gulf of Aden

Synonymy—

- 1854 *Patella variegata* Reeve, Conch. Iconica, pl. 16, figs. 36 a-c. "Australia," in error. (non Reeve, 1842, Conch. Syst., 2, pl. 136, fig. 1).
 1870 *Patella variegata* Reeve (1854), Fischer, J. de Conchyl., 18, p. 167. Suez, Egypt.
 1870 *Helcioniscus variegatus* Reeve, Dall, Amer. Journ. Conch., 6, p. 277, pl. 16, fig. 27 (radula); locality corrected to Red Sea and Gulf of Aqaba).
 1891 *Helcioniscus eucosmia* Pilsbry, Man. Conch., vol. 13, p. 148, pl. 71, figs. 61-64 (non Pilsbry, 1895, Cat. Mar. Moll. Japan, p. 112, pl. 7, figs. 7-10; Japan).

Records—RED SEA; Gulf of Aqaba (Dall, 1870); Ras Banas (AWBP coll.); Berbera, Gulf of Aden (USNM).

Cellana radiata (Born, 1778)

Unfortunately the better-known name for this species, *Patella rota* Gmelin, 1791, must fall as a synonym of *Patella radiata* Born, 1778. No locality was given for Born's species, but without doubt, the shell he described (1778) and figured (1780) is the common Indian and Ceylon form of the limpet known as *rota*.

The overall distribution of *radiata* is East Africa from Natal northward to the Arabian Sea, India, Ceylon, and the Asiatic mainland to southern Japan, the islands of the Indian Ocean, northern Australia, the Philippines, Palau Islands, Solomons down to New Caledonia, and eastward across the Pacific to as far as the Marquesas.

This widely-distributed Indo-Pacific limpet is an exceedingly variable one, but nevertheless

several of the more distinctive variants qualify for consideration as geographical subspecies.

Relevant synonymy and locality data are listed separately under the respective subspecies.

Cellana radiata subspecies radiata (Born, 1778)

(Pl. 67, figs. 8, 9; Pl. 120)

Range—India, Ceylon, West New Guinea and Philippine Islands.

Remarks—In this the assumed typical form of *radiata* the sculpture consists of numerous, narrow, approximately-equal, flat-topped, radial riblets, with linear interspaces. There are no underlying radial folds, and the shape is regularly and broadly ovate. The coloration is exceedingly variable and of no diagnostic significance.

Description—Shell of moderate size, up to 37 mm. (1.7/16 inches) in length, of rather light build, roundly ovate, and with a subcentral nucleus. Sculpture consisting of numerous, regular, narrow, flat-topped radial riblets, separated by linear grooves. Coloration variable, the typical form maculated with 9 to 11 bifid radial streaks in purplish brown, upon a yellowish ground, the spatula chestnut-brown, except when varying clouded with whitish callus. In some examples the radial streaks are broken up into sparse dashes and chevrons. In *forma aster* Reeve, 1855, from unknown locality, the purplish brown radial maculations are about nine, are very broad, and they alternate with narrow yellowish interspaces. In *forma luzonica* Reeve, 1855, from the Philippines, there is a bold radiate pattern of irregular black streaks upon a transparent yellow ground; in *forma scalata* Reeve, 1855, also from the Philippines, most of the radial maculations become forked towards the margin, and in *forma petalata* Reeve, 1854, from North Queensland, Australia, the radial maculations in most examples join up to form a few broad bands.

Measurements (mm.)—

length	width	height	
37.0	33.0	14.0	Galle, Ceylon
31.0	26.0	9.0	Galle, Ceylon
29.0	25.5	11.5	Colombo, Ceylon
25.5	20.0	8.0	Fitzroy Id., N. Queensland
23.0	19.0	10.0	Colombo, Ceylon
21.0	17.0	7.0	Philippines (f. <i>luzonica</i>)

Synonymy—

- 1778 *Patella radiata* Born, Index Revum Nat. Mus. Caes. Vind., p. 443: 1780, pl. 18, fig. 10.
 1791 *Patella rota* Gmelin, Linn. Syst. Nat., ed. 13, 1, p. 3720; based upon Martini-Chemnitz, Conch. Cab., vol. 10, p. 330, pl. 168, fig. 1619. East Indies and (in error) West Indies.

- 1832 *Patella reynaudi* Deshayes, Bellanger's Voy. aux Indes-Orient., Zool., p. 411. Ceylon Atlas, pl. 2, figs. 11, 12.
 1854 *Patella petalata* Reeve, Conch. Iconica, pl. 22, figs. 56a, b. Australia. Dec. 1854.
 1855 *Patella aster* Reeve, Conch. Iconica, pl. 30, figs. 80 a, b. Unknown locality. Jan. 1855.
 1855 *Patella luzonica* Reeve, Conch. Iconica, pl. 31, figs. 86a, b. Luzon Island, Philippines. Jan. 1855.
 1855 *Patella scalata* Reeve, Conch. Iconica, pl. 31, figs. 89 a, b. Philippines. Jan. 1855.
 1855 *Patella nimbus* Reeve, Conch. Iconica, pl. 42, figs. 143 a, b. Unknown locality. May 1855.
 1891 *Helcioniscus reynardi* (sic) Desh., Pilsbry, Man. Conch., vol. 13, p. 130, pl. 66, figs. 94, 95.
 1911 *Acmaea travancorica* Preston, Rec. Indian Mus., vol. 6, p. 39. Travancore, India.
 1911 *Acmaea bombayana* E. A. Smith, Proc. Malac. Soc., London, vol. 9, p. 357, text figs. A-C. Bombay, India.
 1911 *Acmaea bombayana* var. *ceylanica* E. A. Smith, Proc. Malac. Soc., London, vol. 9, p. 358, text fig. D Galle, Ceylon.

Records—INDIA: Bombay (USNM 443304); Varkalay, Travancore (type of *Acmaea travancorica*). CEYLON: Colombo (AWBP coll.); Mt. Lavinia (AWBP coll.); ½ mile S. W. of Dehiwala Village, Colombo (ANSP 224978); Galle (ANSP and AWBP coll.); SABAH: Labuan (Aust. Mus.). WEST NEW GUINEA: Boensaki Island, off Soweik, Soepiori Island, Schouten Islands (AWBP coll.). PHILIPPINES: Gigmoto, Catanduanes Island (ANSP); Luzon Island (type locality of *Patella luzonica*). QUEENSLAND: Cairns; Fitzroy Island (both AWBP coll.).

Cellana radiata subspecies capensis (Gmelin, 1791)

(Pl. 67, figs. 10, 11; Pl. 121)

Range—East coast of South Africa and Natal north to Zanzibar.

Remarks—This subspecies has subobsolete to obsolete radial folds, with a superimposed sculpture of radial riblets that are dense, linear-spaced and granulose to scabrous. The dark-brown radial markings tend to run together to form a few large squarish maculations, and the spatula usually has a dark bar across it near the top, except in heavily callused adults when an orange sinear takes its place.

Gmelin based his species upon "Argenville Conch. pl. 1, fig. 0" and "Kaemmerer Conch. Rudolphi, figs. 1, 2." The Argenville plates are numbered differently in the several editions of that work, so to avoid confusion, Gmelin's second reference, that of Kaemmerer, 1786, pl. 2, figs. 1, 2, is here selected as the basis of the subspecies, and this action is in accord with the generally accepted concept of *capensis* and coincides with the admirable illustrations in Krauss, 1848.

Description—Shell of moderate size, up to 39 mm. (1½ inches) in length, rather lightly built, except in the fully adult; ovate to elongately-ovate, with the anterior end slightly narrowed, depressed

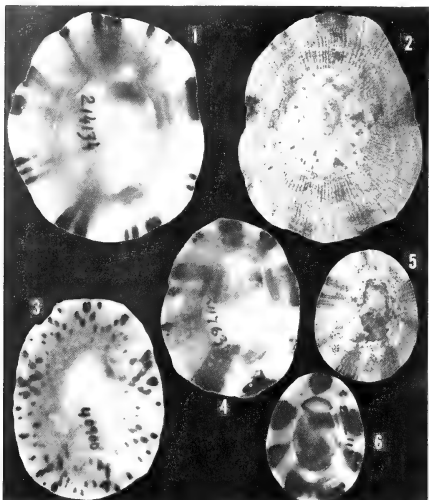


Plate 121. Figs. 1-6. *Cellana radiata* subspecies *capensis* (Gmelin, 1791). Fig. 1. Chukwani Palace, Zanzibar, 35 mm., AWBP coll. 214134. Figs. 2, 3. Kizimkazi, Zanzibar, 31-37 mm., AWBP coll. 40900. Figs. 4-6. Pondoland, South Africa, 24-33 mm., AWBP coll. 211763b.

to moderately elevated, and with the apex varying from subcentral to the anterior third. Sculpture consisting of very numerous, fine, linear-spaced, weakly granulose or scabrous radials. Margin finely denticulated. The nine radial folds, so characteristic of some of the other *radiata* subspecies, are subobsolete to obsolete in *capensis*. Colour of interior, yellowish with a silvery lustre, an orange to chestnut-brown spatula, and a few broad radial rays of dark purplish brown. Almost invariably the spatula has a dark-brown blob, running in from the right, at just below the constriction. Fully adult and senile examples often have the spatula obliterated by a whitish callus, and in these there is usually a smear of bright-orange at the head end of the spatula.

Measurements (mm.).—

length	width	height	
39.0	29.0	—	Pilsbry, 1891, p. 146
37.0	29.0	12.5	S. W. Zanzibar
33.0	26.0	14.0	Pondoland
28.0	23.5	8.5	Port Edward, Natal

Synonymy—

- 1791 *Patella capensis* Gmelin, Syst. Nat. ed. 13, p. 3720, based upon Kaemmerer, Conch. Rudolphi, pl. 2, figs. 1, 2.

- 1842 *Patella variegata* Reeve, Conch. Systematica, vol. 2, p. 15, pl. 136, fig. 1.
 1848 *Patella capensis* Gmelin, Krauss, Stüdfr. Moll., Stuttgart, p. 53, pl. 3, fig. 13.
 1891 *Helcioniscus capensis* Gmelin, Pilsbry, Man. Conch., vol. 13, p. 146, pl. 16, figs. 15-17.
 1948 *Cellana capensis* Gmelin, Stephenson, Ann. Natal Mus., vol. 11 (2), pp. 279, 282; text fig. 11 (radula).

Records—SOUTH AFRICA: "Cape of Good Hope" (type locality); Coffee Bay, 1 mile S. of Umtata River, Transkei (V. Orr, 1955; ANSP); Port St. Johns, Pondoland (V. Orr, 1955; ANSP); Port Edward, Natal (V. Orr, 1955; ANSP) near Durban (Mrs. N. Prior); ZANZIBAR: Dembani, 2 miles N. of Kizimkazi (AWBP coll.); Chukwani Palace (ANSP); Mangapwani (ANSP).

Cellana radiata subspecies *enneagona* (Reeve, 1854)

(Pl. 67, fig. 14; Pl. 121)

Range—Madagascar, Andaman Islands, Indonesia, Philippines and Bonin Islands, Japan.

Remarks—The elongated, narrowly ovate shape, nine prominent radial folds, and irregularly indented margin, characterise this form or subspecies.

Description—Shell moderately large, up to 53 mm. (2½ inches) in length but usually smaller, narrowly ovate to irregularly angular, with the apex between the center and the anterior third. Sculpture consisting of 9 conspicuous, rounded, radial folds. The entire surface, folds and interspaces alike, is crowded with narrow, crisp radial cords that are rendered slightly scabrous by concentric growth lines. Margin of shell irregular, being strongly projecting at the terminal points of the radial folds, and concave in the interspaces. Colour pattern of interior variable, consisting of radial dark purplish brown streaks upon a pale creamy ground, or the streaks may either ramify towards the margin or break up into tessellated patterns. Usually there are 9 narrow radial areas free from colour pattern, and these correspond to the external folds. Spatula long and narrow, dark-chestnut, sometimes white-callused to a varying degree.

Measurements (mm.).—

length	width	height	
53.5	43.0	13.5	Jackson Beach, Bonin Islands
39.0	32.0	10.5	Jolo, Philippines
30.0	21.0	5.5	Catbalogan, Philippines
25.0	20.0	6.0	Andaman Islands

Synonymy—

- 1854 *Patella enneagona* Reeve, Conch. Iconica, pl. 18, figs. 44a, b. Unknown locality. Dec. 1854.
 1855 *Patella articulata* Reeve, Conch. Iconica, pl. 33, figs. 97 a, b. Island of Ticao, Philippines. Mar. 1855.
 1891 *Helcioniscus enneagona* Reeve, Pilsbry, Man. Conch., vol. 13, p. 152, pl. 28, figs. 35, 36.
 1891 *Helcioniscus articulatus* Reeve, Pilsbry, Man. Conch., vol. 13, p. 128, pl. 65, figs. 87, 88.
 1959 *Cellana enneagona* Reeve, Oyama and Takemura, The Moll. Shells, vol. 3, *Cellana*, pl. 2, figs. 6-8.

Types—Three syntypes of *articulata* are in the British Museum (Natural History).

Records—MADAGASCAR: Pointe Ambarionaambi, S. E. of Nossi Be' (ANSP); Nosi Antsaibory, N. W. Nossi Be' (ANSP); Nosi Tanikely, 4 miles S. of Nossi Be' (ANSP); Pte du Cratere, S. W. Nossi Be' (ANSP); Nossi Iranja, 32 miles S. W. of Nossi Be' (ANSP). ANDAMAN ISLANDS: Port Blair (AWBP coll.). INDONESIA: Bali (AWBP coll.). PHILIPPINES: Ticao Island (type of *articulata*); Cabacben, S. E. Bataan, Luzon Island, rocky shore (ANSP); Iba, Zambales, Luzon (ANSP); Jolo (USNM); Catbalogan, Samar (USNM). JAPAN: Jackson Beach, Bonin Islands (USNM).

***Cellana radiata* subspecies
orientalis (Pilsbry, 1891)**

(Pl. 67, figs. 12, 13; Pls. 123 and 124)

Range—Indonesia, New Guinea, North Western Australia, southern Japan, Palau Islands, Solomon Islands, New Caledonia, Loyalty Islands, Fiji, Tonga, Samoa and Marquesas Islands.

Remarks—This subspecies or form differs from the typical one in the presence of very distinct radial folds that underlie the normal radial sculpture. The colour pattern is variable, ranging from buff with sparse dark-brown chevrons, to broad radial dark stripes, each one occupying an interspace. It is likely that the latter colour form is *Patella tessellata* Hombron & Jacquinot, 1841, preoccupied, and later renamed *Patella hombroni* Dautzenberg & Bouge, 1933. Unfortunately I am unable to verify the identity of *hombroni* since

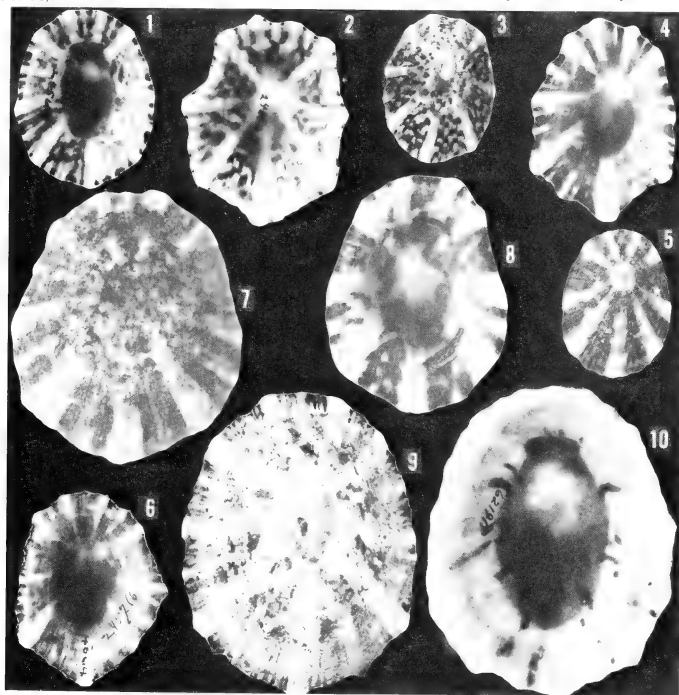


Plate 122. Figs. 1-10. *Cellana radiata* subspecies *enneagona* (Reeve, 1854). Figs. 1-3. Jolo, Philippines, 25-39 mm., USNM 245600. Figs. 4-6. Janelo Bay, Luzon, Philippines, 27-36 mm., AWBP coll. 48214. Figs. 7, 8. Pointe Ambarionaambi, Nossi

Be', Madagascar, 30-36 mm., AWBP coll. 48742. Figs. 9, 10. Jackson Beach, Bonin Islands, Japan, 40-53.5 mm., AWBP coll. 621911.

the Lesson types were not available at the time of writing.

Description—Shell of moderate size, up to 41.5 mm. (1½ inches) in length, rather solid, roundly ovate, and with a subcentral nucleus. The dense linear-spaced radial riblets are superimposed upon an underlying sculpture of bold, distant, radial folds, 11 or more in number, and these strongly corrugate the margin. The coloration is variable. In the typical form the radiating dark-brown lines or streaks tend to anastomose towards the margin, there forming a series of rectangular blotches. In the *eudora* form the dark markings are small, sparse, often chevron-shaped, and they show through to the interior, which varies from buff to bright lemon-yellow. This form is widely distributed, ranging from Java to Japan and down through the Solomons to New Caledonia. In the form from the eastern extremity of the *radiata*

range, Samoa and the Marquesas Islands, the radial lines of the interior tend to run together and form broad, dark-brown, radial maculations, corresponding to the interspaces of the external radial folds.

Measurements (mm.)—

length	width	height	
41.5	36.0	11.5	Marquesas Islands
34.5	30.0	15.0	holotype of <i>orientalis</i>
32.0	27.5	9.0	Tau Id., Samoa
28.0	25.0	12.0	holotype of <i>eudora</i>
24.0	20.5	7.0	Russell Ids., Solomons

Radula—The radula is typical of *Cellana*, with a very weak and small medio-central vestigial plate between a pair of long, narrow, fully-developed centrals that curve forward tangentially above, and alternate with a pair of broader laterals, that are wider-spaced. Both the centrals and the laterals are indented along one edge to form two or three cusps.

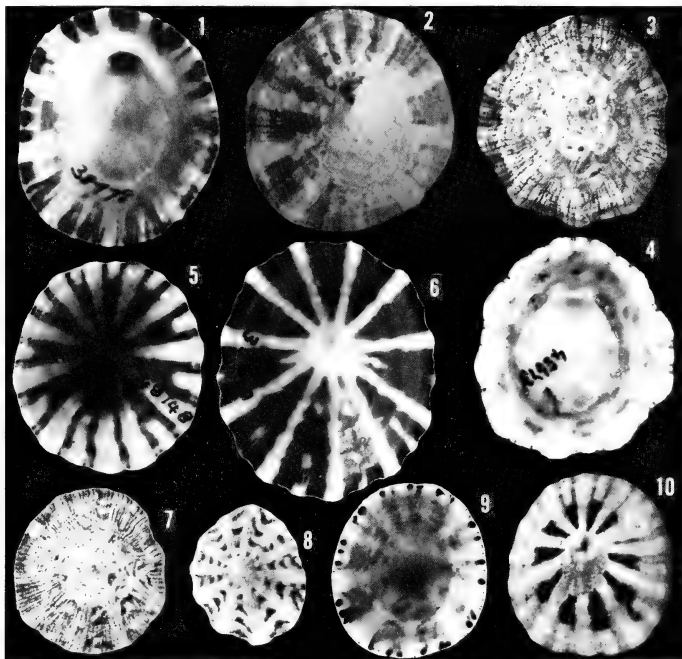


Plate 123. Figs. 1-10. *Cellana radiata* subspecies *orientalis* (Pilsbry, 1891). Fig. 1. Fiji, 34.5 mm. (lectotype of *orientalis*). ANSP. Fig. 2. (paralectotype of *orientalis*). ANSP. Figs. 3, 4. Lifu, Loyalty Islands, 27 mm. (*eudora* form), AWBP coll. 45673. Fig. 5. Niuaufu Island, Tongan Group,

27 mm., AWBP coll. 48748. Fig. 6. Tau Island, Manua Group, Samoa, 32 mm., USNM 513368. Figs. 7-9. Lingatu Point, Banika Island, Russell Islands, Solomon Islands, 15-27 mm., Domin. Mus. Fig. 10. Tonga, 23.5 mm., AWBP coll. 25349.

Synonymy—

- †1841 *Patella tessellata* Hombron & Jacquinot, Ann. Sci. Nat., Zool. & Paleont., ser. 2, vol. 16, p. 190 Mangareva. (non O. F. Müller, 1779).
- 1891 *Helcioniscus rota* var. *orientalis* Pilsbry, Man. Conch., vol. 13, p. 146, pl. 72, figs. 76, 77. Fiji.
- †1933 *Patella hombroni* Dautzenberg & Bouge, J. de Conchyl., vol. 77, p. 416 (nom. nov. pro. *P. tessellata* H. & J., 1841).
- 1938 *Cellana rota*: Adam & Leloup, Mem. Mus. Roy. D'Hist. Nat. Belg., vol. 2, pt. 19, p. 12, pl. 2, fig. 3 (shell), text fig. 3 (radula). Java.
- 1940 *Cellana eudora* Iredale, Aust. Zool., vol. 9, pt. 4, p. 433, pl. 33, figs. 13-15, Lifu, Loyalty Islands.
- 1959 *Cellana rota*: Oyama & Takemura, The Moll. Shells, vol. 3, *Cellana*, pl. 2, figs. 3-5. Japan.
- 1964 *Cellana rota*: Habe, Shells of Western Pacific in colour, vol. 2, pl. 3, fig. 5. Japan.

Types—Lectotype, Pilsbry's figured specimen of *orientalis*, here selected, and three syntypes, in the Academy of Natural Sciences of Philadelphia. Holotype of *eudora* in the Australian Museum, Sydney.

Records—JAPAN: Amami Islands (Habe, 1964). GUAM (USNM); PALAU ISLANDS: S. E. end of Eil Malk (ANSP). INDONESIA: Java (Adam & Leloup, 1938). N. W. AUSTRALIA: Vansittart Bay (Aust. Mus.); SOLOMON ISLANDS: Lingatu Point, Banika Island, Russell Islands, high tide on coral rock (Domin. Mus.); coast near Kopiu, southern Guadalcanal, on exposed rock platform (Domin. Mus.); Ysabel (Aust. Mus.). NEW CALEDONIA: N. of Toula (AWBP coll.); La Roche Percée, Bourail (ANSP). LOYALTY ISLANDS: Lifu (type locality of *eudora*). TONGA: (AWBP coll.); Nuafoou Island (AWBP coll.). FIJI: (type locality of *orientalis*). MAR-

QUESAS ISLANDS: Atuona Bay, Hivaoa Island (H. A. Pilsbry, Pinchot Exped., 1929; AWBP coll.); Taiohae, Nukuhiva Island (H. A. Pilsbry, Pinchot Exped., 1929; ANSP). SAMOA: Tau Island, Manua Group (USNM).

Cellana deformis (K. Martin, 1883)

Range—Miocene of Tiji Taon, Java.

Remarks—This species is inadequately illustrated by a side elevation only. It shows marked corrugations, similar to those of *Cellana radiata* subspecies *orientalis* (Pilsbry, 1891), but until the type material is examined, an exact evaluation of the species cannot be made.

Synonymy—

- 1883 *Patella deformis* K. Martin, Samml. Geol. Reichs-mus. Leiden, vol. 1, p. 236, pl. 11, fig. 31.

Cellana karachiensis (Winckworth, 1930)

(Pl. 126)

Range—Gulf of Oman to Pakistan.

Remarks—This species seems to be nearest to *livescens* Reeve, 1855 (formerly *cernica* H. Adams, 1869) from Mauritius which also has 9-10 broad radiate bands of dark reddish brown, upon a yellowish ground, as well as a moderate development of the 9-folds. *P. livescens*, however, is more elongately ovate, and flatter, with the apex at about the anterior third.

Description—Shell rather large, up to 57 mm. (2¼ inches) in length, broadly ovate, slightly narrowed in front, and moderately elevated, with rounded slopes, and a subcentral nucleus; margin smooth to very weakly crenulated. Sculpture of dense, crisp, radial riblets, rendered granulose by concentric growth lines; riblets varying between 120 and 180, with about 20 of them slightly stronger than the rest, and in some examples there is a subobsolete indication of the "9-fold" state, reminiscent of the *enneagona* subspecies of *radiata*. Colour of exterior, pale brownish-buff, with eleven broad radiate bands of deep reddish-brown; internally the spatula is chestnut-brown, often clouded over with pale fawn callus, and surrounding the spatula is a zone of yellow, merging with silver towards the margin, the external brown pattern showing through; juveniles have a sparse pattern of radiate reddish-brown dashes on a yellowish ground.

Measurements (mm.)—

length	width	height
57.0	46.5	20.0
42.0	36.7	17.5
41.5	30.0	12.0
35.0	29.0	15.0
		holotype

Plate 124. *Cellana radiata* subspecies *orientalis* (Pilsbry). Fig. 1. Banika Island, Russell Islands, Solomons. Radula. Fig. 2. Bali, Indonesia. Radula, from Adam and Leloup, 1938, p. 13, fig. 3 (as *rota* Gmelin).

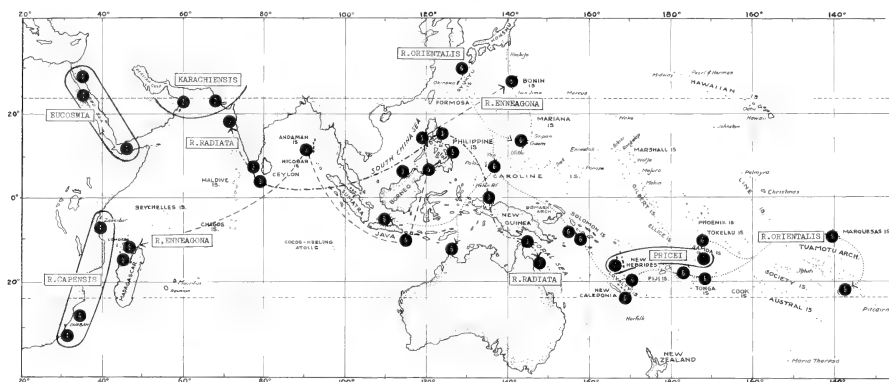


Plate 125. Geographical distribution of *Cellana radiata* (Born), its subspecies and related species. Fig. 1. *Cellana euosmia* (Pilsbry). Fig. 2. *Cellana karachiensis* (Winckworth). Fig. 3. *Cellana radiata* (Born). Fig. 4. *Cellana radiata* sub-

species *capensis* (Gmelin). Fig. 5. *Cellana radiata* subspecies *cuneigona* (Reeve). Fig. 6. *Cellana radiata* subspecies *orientalis* (Pilsbry). Fig. 7. *Cellana pricei* Powell (new species).

Synonymy—

1930 *Patella capensis karachiensis* Winckworth, Proc. Malac. Soc., London, vol. 19 (2), p. 80. Not figured.

Types—Holotype and paratype in the British Museum (Natural History).

Records—PAKISTAN: East Pier, Karachi (type locality); oyster rocks, Karachi (Winckworth coll., British Mus. (Nat. Hist.)); GULF OF OMAN: Muscat (ex. Winckworth; AWBP coll.).

Cellana livescens (Reeve, 1855)

(Pl. 127)

Range—Mauritius.

Remarks—This is a moderately large, rather thin-shelled limpet of low elevation, easily recog-

nised by its striking colour pattern of nine broad purplish brown radial bands, separated by narrow golden-yellow rays; there is a whitish spatula, and the whole of the interior is highly iridescent. It is regrettable that *cernica*, type of the genus *Cellana*, must fall as a synonym of *livescens*, described in error from Mazatlan, west Mexico, but in reality the well-known Mauritian limpet.

Description—Shell moderately large, up to 51 mm. (2 inches) in length, rather flat, elongately ovate, with a weakly scalloped margin, and a flattened apex at about the anterior third. Sculpture consisting of about 100 or more fine, crisp, slightly scabrous radials of varying sizes, and in addition there are the 9 broadly rounded, radial

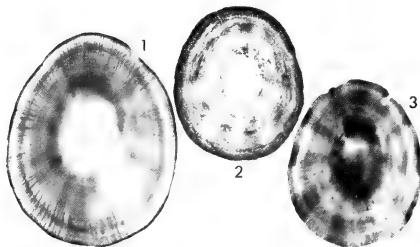


Plate 126. Figs. 1-3. *Cellana karachiensis* (Winckworth, 1930). Fig. 1. Karachi, Pakistan, 57 mm., AWBP coll. 46136. Figs. 2, 3. Muscat, Gulf of Oman, 41 mm., AWBP coll. 46142.

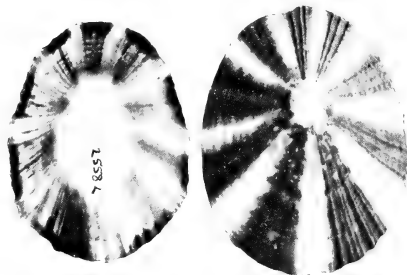


Plate 127. *Cellana livescens* (Reeve, 1855), Mauritius, 34-40 mm., AWBP coll. 25582.

fold, similar to those of the *enneagona* sub-species of *radiata*; although little raised, these folds are quite distinct in all the material examined. Colour of exterior, olive to pinkish grey, with 9 broad, radiate bands of dark purplish brown; internally the spatula is white to bluish-grey, the remaining area with the external purplish brown radials showing through strongly; the narrow interspaces, corresponding to the external folds, are bright golden-yellow; the whole highly iridescent.

Measurements (mm.)—

length	width	height	
51.0	41.0	12.5	Mauritius
39.0	29.0	10.0	Mauritius holotype
36.0	28.0	10.0	Mauritius

Synonymy—

- 1834 *Patella novemradiata* Quoy and Gaimard, Voy. "Astrolabe," Zool., vol. 3, p. 346, Mauritius. (non G. Fischer, 1807).
 1855 *Patella livescens* Reeve, Conch. Iconica, pl. 29, figs. 75 a, b. "Mazatlan, Gulf of California," in error. June 1855.
 1869 *Nacella (Cellana) cernica* H. Adams, Proc. Zool. Soc., London, p. 273, pl. 19, figs. 7, 7a. Barkly Island, Mauritius.
 1891 *Helcioniscus novemradiatus* Quoy and Gaimard, Pilsbry, Man. Conch., vol. 13, p. 146, pl. 30, figs. 55-58.
 1891 *Helcioniscus livescens* Reeve, Pilsbry, Man. Conch., vol. 13, p. 149, pl. 71, figs. 59, 60.
 1891 *Helcioniscus livescens* Reeve, Pilsbry, Man. Conch., vol. 13, p. 152, pl. 73, figs. 99, 100.

Types—The type specimens of *livescens* should be in the British Museum (Natural History) but I have not been able to locate them.

Records—MAURITIUS: Barkly Island (type locality); AWBP coll.

Cellana pricei Powell new species

(Pl. 128)

Range—Samoa and New Hebrides.

Remarks—This species is easily recognised by its dark silvery grey to greenish black colour, relieved by short marginal white streaks at the extremities of the primary radials. Apparently the species is restricted in habitat to dark volcanic rock. The relationship is with the *radiata* series, but the shell is sufficiently distinct, particularly in sculpture, to discount the possibility of it being merely an ecotype.

Description—Shell of moderate size, 35.6 mm. (1½ inches) in length, ovate, with irregularly corrugated margins, depressed, with the apex varying between subcentral and the anterior third. Sculpture rather coarse and irregular, of rounded radial ribs, 14 or 15 of them of primary strength, and these project at the margins, slightly more than do the corrugations between them. The whole surface is crossed by dense crisp sublammellose concentric lirae. Colour of exterior greenish black, with an elongated white streak towards the margin upon most of the primary radials; interior dark silvery grey, with the spatula dark olive-brown, clouded in part by a bluish white callus. The marginal white streaks of the exterior show through strongly upon the inner surface.

Types—The holotype is in the Auckland Museum (TM.1337).

Measurements (mm.)—

length	width	height	
35.6	28.0	8.5	holotype
27.0	21.75	7.0	paratype

Records—WESTERN SAMOA: Upolu, half-tide near Apia, on black volcanic rocks (L. Price, 1964); Upolu (Col. R. W. Tate, 1920; Domin. Mus. MF. 83). NEW HEBRIDES: reef near hotel, Tanna (W. F. Ponder, 1968).

Cellana garconi (Deshayes, 1863)

(Pls. 129, 130, 132)

Range—Island of Reunion and northern Madagascar.

Remarks—The writer has seen neither the type nor a photograph of this species. The type was not available at the time of writing, owing to reorganisation of the collections of the Muséum National d'Histoire Naturelle, Paris. It is not certain that the type is located in the collections of that institution.

However Deshayes' excellent illustrations show a shell very similar to a common shell from northern Madagascar, the only marked difference being in the position of the apex, which is shown

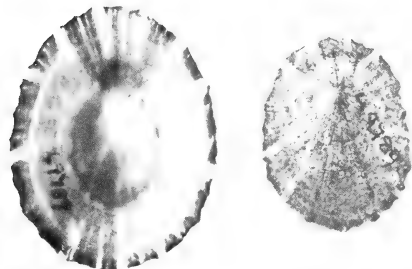


Plate 128. *Cellana pricei* Powell, new species, near Apia, Upolu, Samoa. Holotype, 35.6 mm. and paratype, 27 mm.

near central in Deshayes' figures but is at about the anterior fourth or fifth in Madagascar shells. Deshayes' shell is tall-conic, but the Madagascar shells are very depressed. However the position of the apex, which is to a great extent governed by the altitude of the shell, varies considerably within many species of limpets, and is therefore of little taxonomic importance.

Upon the assumption that the Madagascar shells represent *garconi*, then that species appears to be related to the Indo-Pacific *testudinaria* and represents a western offshoot of that species, just as *vitiensis* (= *sagittata*) is an eastern outlier in the Pacific.

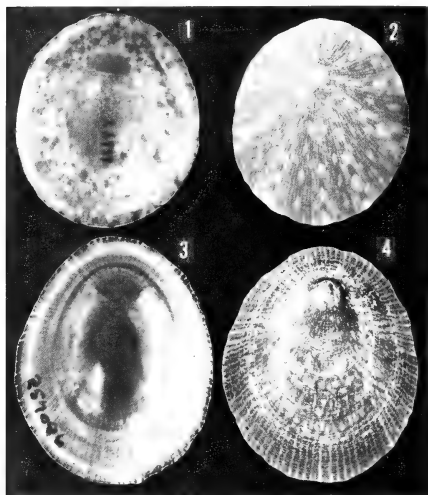


Plate 129. Figs. 1, 2. *Cellana vitiensis* Powell, new name pro *Patella sagittata* Gould, 1846, non Donovan, 1820; Fiji, 34 mm., AWBP coll. 26939. Figs. 3, 4. *Cellana garconi* (Deshayes, 1863). Nossi Be', Madagascar, 31.5 mm., AWBP coll. 257086.

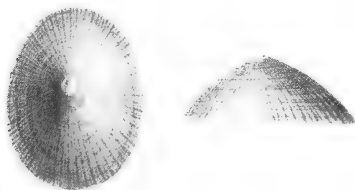


Plate 130. *Cellana garconi* (Deshayes, 1863), Island of Reunion. Original figures from Deshayes, Moll. de l'Île Réunion, pl. 6, figs. 11, 12.

The main differences in *garconi*, compared with *testudinaria*, are the smaller, more lightly built shell, with dense more definite sculpture, the radials being very numerous, and bearing distinct ovate granules; also the shell tends to be narrow in front, and never has the chevroned or tortoise-shell markings of *testudinaria*.

Description (translation from Pilsbry, 1891, l. c.).—Shell "regularly oval, conoidal, the summit elevated, pointed, very slightly directed forward, situated at the front two-fifths of the length. From the apex radiate a great number of very fine, regular, rather equal riblets, which bear long, obtuse granules. The margins are simple and sharp. The interior lined with very bright nacre of a whitish-brown, the central callus quite large, white, sharply defined by the muscle-scar. The shell is thin, semi-transparent, of a uniform brown-blackish, but if held up toward the light, a few rays of a beautiful red become visible."

Measurements (mm.).—

length	width	height
31.0	25.7	7.0
25.0	19.5	5.0
23.0	19.0	9.0

type of *garconi*

Radula (Nossi Be' specimen).—Very similar to that of *testudinaria*, except for the lateral, which is short, broadly arched and expanded above, and very deeply notched.

Synonymy.—

1863 *Patella garconi* Deshayes, Moll. de l'Île Réunion, p. 42, pl. 6, figs. 11, 12.

1891 *Helcioniscus garconi*: Pilsbry, Man. Conch., vol. 13, p. 150, pl. 66, figs. 100, 101.

Records.—ISLAND OF REUNION (type locality). MADAGASCAR; south side of Nossi Iranja, 32 mi. S. W. of Nossi Be' (ANSP Exped. Sept.-Oct. 1960); Pte. du Cratère, S. W. Nossi Be' (ANSP); between Ambatoloaka and Madirokely, S. W. Nossi Be' (ANSP).

***Cellana testudinaria* (Linnaeus, 1758)**

(Pl. 67, figs. 1, 2; Pl. 131; Pl. 132, fig. 1)

Range.—Andaman Islands to the Ryukyu Islands and to New Caledonia and North Queensland.

Remarks.—This is a large, solid, broadly ovate, and rather depressed *Cellana*, externally rather smooth, of brownish slate colour, radially patterned in darker brown, and bluish silvery within. This widely distributed Indo-Pacific species is almost invariably associated with dark volcanic rock, and occurs near and below low tide in exposed situations. Pilsbry's *Helcioniscus rota* var. *discrepans* proves to be a synonym of *testudinaria*. The type material consists of two undersized,

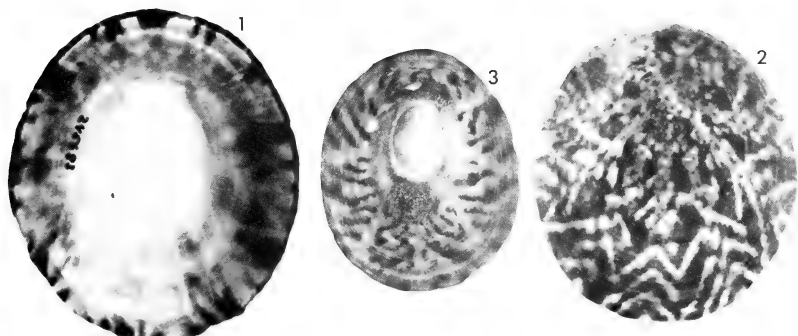


Plate 131. Figs. 1-3. *Cellana testudinaria* (Linnaeus, 1758). Figs. 1, 2. Port Tilig, Lubang, Philippine Islands, 73.5 mm., USNM 245683. Fig. 3. Lectotype of *Helcioniscus rota* var.

discrepans Filsbry, 1891, 29 mm.; an eroded young *testudinaria* from unknown locality.

badly worn examples from unknown locality. Another synonym is Dunker's *insignis* which Fraunfeld claimed as coming from the Cape of Good Hope, but almost certainly incorrectly. Fraunfeld's figure looks like *testudinaria*, but there is no other record of the species from that area.

Two related smaller species, also with a preference for dark volcanic rock, extend the range of the *testudinaria* type of *Cellana*, to the westward in *garconi* of the Madagascar-Reunion area, and to the eastward in *vitiensis*, the latter apparently being restricted to the Fiji Islands.

Description—Shell solid, reaching a large size, up to 90 mm. (3½ inches) in length, but most adults about two thirds that size; broadly ovate, of low rounded profile, with the apex at about the anterior third; margin simple and smooth. External sculpture consisting of weak to obsolete, low, narrow, smooth radial riblets. Colour of exterior dark greenish brown, with a radiate pattern in dark brown, within the shell substance, and apparent only when the shell is held to the light; the pattern may consist of radial streaks, joined across in a netted pattern, or it may consist of bold chevrons; internally the shell is bluish silvery, with the large elongated spatula greyish white to yellowish brown; the margin of the shell has a continuous border in dark-brown, with terminal blotches from the internal radial pattern which also shows through faintly, back almost to the spatula.

Measurements (mm.)— (all AWBP coll.).

length	width	height	
90.0	77.0	33.0	Bongao, Sulu Archipelago
79.0	67.0	27.0	Melanesia
73.5	64.0	18.0	Lubang, Philippines
65.0	56.0	15.0	Raga, New Hebrides
53.0	43.0	14.5	Bataan, Philippines
30.5	24.5	6.5	near Noumea, New Caledonia

Plate 132. Fig. 1. *Cellana testudinaria* (Linnaeus), Java. Radula, from Adam & Leloup, Mem. Mus. Roy. D'Hist. Nat. Belg., vol. 2 (19), p. 12. Fig. 2. Lateral tooth of *Cellana vitiensis* Powell (new name), Fiji. Fig. 3. Lateral tooth of *Cellana garconi* (Deshayes), Nossi Bé, Madagascar.

Radula—All teeth long and narrow; paired

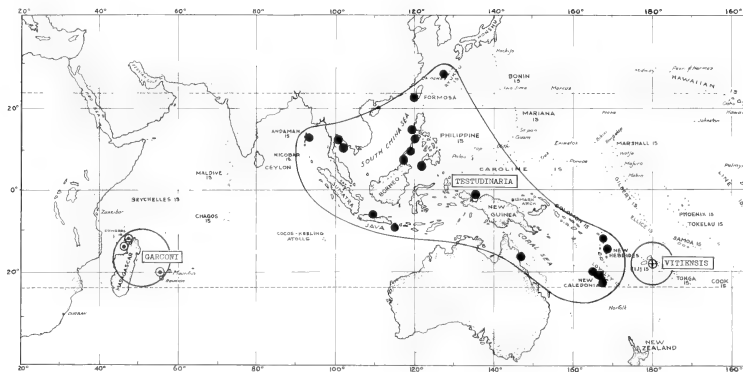


Plate 133. Geographical distribution of *Cellana testudinaria* (Linnaeus), *Cellana garconi* (Deshayes) and *Cellana vitiensis* Powell (new name).

centrals each with a long slender, erect, simple-pointed cusp; paired laterals larger than the centrals, each with the cusp moderately curved, ending in a sharp point, and with a weak denticle on each side, at the base of the cusp, and at a point just above middle height of the whole tooth; marginals 3, outer two more or less fused basally, and with a rudimentary cusp on the middle one only.

Synonymy—

- 1758 *Patella testudinaria* Linnaeus, Syst. Nat., ed. 10, p. 783. Locality?
 1765 "Lepas ou Patelle," Argenville, Conch. Traité Gén. Coq. de Mer, ed. 2, pl. 2, fig. P.
 1798 *Patella patera* Röding, Mus. Bolten., vol. 2, p. 8.
 1825 *Patella rumphii* Blainville, Dict. Sci. Nat., 38, p. 95.
 1854 *Patella testudinaria* Linne', Reeve, Conch. Iconica, pl. 4, figs. 6 a, b.
 1866 *Patella insignis* Dunker, Verh. Zool.-bot. Gesell., Wien, p. 941.
 1868 *Patella insignis* Dunker, Fraumfeld, Reise der Novara, Zool. Moll. p. 14, pl. 2, fig. 25.
 1891 *Helcioniscus testudinaria* Linne', Pilsbry, Man. Conch., vol. 13, p. 128, pl. 25, figs. 16-19.
 1891 *Helcioniscus rota* var. *discrepans* Pilsbry, Man. Conch., vol. 13, p. 146, pl. 72, figs. 78-80.
 1906 *Helcioniscus mestayerae* Suter, Trans. N. Z. Inst., vol. 38, p. 322, pl. 18, figs. 7-9. "Stewart Island, New Zealand," in error.
 1938 *Cellana testudinaria* Linne', Adam & Leloup, Mém. Mus. Roy. D'Hist. Nat. Belg., vol. 2 (19), p. 10; p. 12, fig. 2 (radula).
 1959 *Cellana testudinaria* Linne', Oyama & Takemura, Moll. Shells, vol. 3, *Patella-Cellana*, pl. 1, figs. 7-10.

Types—The figured holotype and the paratype of *discrepans* are in the Academy of Natural

Sciences of Philadelphia, and the holotype of *mestayerae* is in the Dominion Museum, Wellington, New Zealand.

Records—ANDAMAN ISLANDS: Port Blair (AWBP coll.). INDONESIA: Java, Amboina, Bali (Adam and Leloup, 1938). SABAH (BORNEO): Marudu Bay, on surf washed rocks at mid to low tide (USNM). NEW GUINEA: Samberbaba, Japen Island (ANSP. Exped. 1956: ANSP). GULF OF SIAM: Koh Chang (USNM); Koh Kut (USNM). SULU ARCHIPELAGO: Bongao Islands (USNM). PHILIPPINES: west coast, Palau Island, Luzon (USNM); Marivales, Bataan, Luzon (du Pont-Acad. Exped. 1955: ANSP); Iba, Zambales, Luzon (du Pont-Acad. Exped. 1955: ANSP); Jamelo Bay, Luzon (USNM); Port Tilig, Lubang (USNM); Gignoto, Catanduanes Island (du Pont-Acad. Exped. 1955: ANSP); Cuyo Island, Palawan (ANSP). TAIWAN (FORMOSA): (USNM). RYUKYU ISLANDS (USNM); Nase, Okinawa (AWBP coll.). BANKS ISLANDS: Vanualava (AWBP coll. 186). SANTA CRUZ ISLANDS: Vanikoro (A. T. Pycroft, 1932, Auck. Mus.). NEW HEBRIDES: Lamap, Mallicolo Island (ANSP); Steepcliff Bay, Pentecost, Raga (AWBP coll.); Aoba (AWBP coll.); Gaua (A. T. Pycroft, 1932, Auck. Mus.); Vureas (A. T. Pycroft, 1932, Auck. Mus.). NEW CALEDONIA: Baie des Prunes near Noumea (G. & M. Kline, 1958: ANSP); near Amos, N. E. coast, under smooth basalt boulders, in caverns (L. Price, 1969). AUSTRALIA: Queensland: Cairns (AWBP coll.).

Cellana vitiensis Powell new name

(Pl. 129, figs. 1, 2; Pl. 132, fig. 2)

Range—Fiji Islands.

Remarks—Unfortunately the name *Patella sagittata* Gould, 1846, is preoccupied by the same combination used by Donovan, 1820, in Rees' Encyclopaedia of Conchology. Donovan's "*P. sagittata*" appears in the encyclopaedia against a rather crude figure at the top left of plate 10 in volume 5, and according to Dr. J. D. Taylor of the British Museum (Natural History) there ap-

pears to be no other reference to the name in the text. Nevertheless Donovan's name qualifies as validly published, and a new name for Gould's species becomes necessary since no substitute name for the apparently endemic Fijian species is available.

The Fijian species has often been mistaken for the young of *testudinaria*, but examples of that species of comparable size are more elongate, of greater solidity, lie perfectly flat, the radial sculpture is weaker and it does not develop granules. A constant feature of *vitiensis* is the anterior and posterior concavities of the shell margin, so that when the shell is placed upon a flat surface it can be rocked in a fore and aft motion.

The large *Cellana testudinaria* does not seem to occur in Fiji, or elsewhere east of there.

Description—Shell rather small, up to 39 mm. (1½ inches) in length but usually much smaller, of light build, broadly ovate, and of rather low profile, the apex at about the anterior fourth, and inclined forward; margin thin and sharp, without crenulations. There is a broad but slight concavity in the shell margin both anteriorly and posteriorly, and laterally the margin is slightly broadly convex. Sculpture crisp and delicate, consisting of densely-packed linear-spaced radials, all of which are closely granulose. Colour of exterior dark-brown to bluish black, obscurely rayed with pale blue-green tessellations. When held to the light there is an inner pattern of dark reddish brown, composed mainly of anastomosing chevrons. Interior leaden-silvery, with a very narrow blackish margin, and chestnut spatula, often with ill-defined outlines.

Radula—Similar to that of *garconi* but the top of the lateral is longer and less arched.

Measurements (mm.)—

length	width	height	
37.0	32.00	9.0	Fiji
33.5	30.75	11.0	Viti Levu Bay, Fiji
30.0	26.00	7.5	Viti Levu Bay, Fiji

Synonymy—

- 1846 *Patella sagittata* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 148 (non Donovan, 1820).
 1852 *Patella sagittata* Gould, U. S. Explor. Exped., vol. 12, p. 337, pl. 29, figs. 449 a-c.
 1891 *Helcioniscus sagittatus* Gould, Pilsbry, Man. Conch., vol. 13, p. 130, pl. 65, figs. 89-92.

Types—Holotype and three paratypes in the United States National Museum, Washington; USNM, 5839.

Records—FIJI (type locality); "Mbega"=Bega Island ANSP; Viti Levu Bay, N. E. Viti Levu Island, on smooth dark lava rock in the upper tidal zone (W. O. Cernohorsky coll.).

Cellana grata (Gould, 1859)

(Pl. 67, fig. 7; Pl. 134)

Range—Japan and Korea.

Remarks—This common Japanese limpet has often appeared in the literature under the name of *eucosmia* Pilsbry, 1891, which name was first applied to a Red Sea shell, and then later misapplied by Pilsbry, 1895, exclusively to a Japanese *Cellana*. This latter *Cellana* is a synonym of *stearnsii* Pilsbry, 1891, which is a more strongly sculptured form of the false '*eucosmia*' of Pilsbry, 1895. However, *stearnsii* also, must be relegated to the synonymy of *grata* Gould, 1859, which becomes the valid name for this Japanese shell. Gould's *grata* is easily recognised by its rather narrowly ovate outline, high profile, and prominent sculpture of numerous scaly to tubercled radial ribs. The exterior of the shell is greyish, with dashes and speckles in light to dark reddish-brown. These intermittent radial maculations show strongly in the interior, which also has a clear cut spatula of reddish chestnut, deepening to dark-brown at the edges.

Description—Shell of moderate to fairly large size, 30-56 mm. (1½-2¼ inches) in length, ovate to

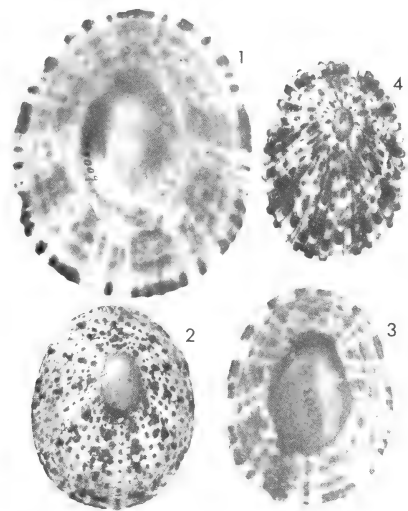


Plate 134. *Cellana grata* (Gould, 1859), Japan, Fig. 1 Suwanosajima, Osumi, 56 mm., USNM 344009. Figs. 2, 3. Nagoya, Kii, 35 and 35.5 mm., AWBP coll. 20276. Fig. 4. Tosa, 34.5 mm. (*stearnsii* form), AWBP coll. 234298.

rather narrowly ovate and moderately elevated, with both anterior and posterior slopes, slightly to conspicuously arched. Sculpture consisting of very numerous scaly to imbricately tuberculose radial ribs which are variable in development; the form *stearnsii* having optimum coarse ribbing. Colour of exterior whitish to dull gray, maculated with reddish brown spots and dashes; interior bluish grey or buff, heavily radially maculated with intermittent dark-brown rays and spots, the spatula bright-chestnut in the middle, but deepening to a dark-brown clear-cut outer edge.

Measurements (mm.)—

length	width	height	
56.0	47.0	27.0	Suwanosejima
50.5	40.5	25.0	Matsushima Id., Korea
38.0	29.0	21.0	holotype of <i>stearnsii</i> , Kii
34.0	25.0	16.0	Tosa, Japan
30.0	24.0	14.0	lectotype of <i>grata</i> ; USNM 1965.
30.0	23.0	11.5	Misaki, Japan

Synonymy—

- 1859 *Patella grata* Gould, Proc. Boston Soc. Nat. Hist., vol. 7, p. 161.
 1891 *Patella (Helcioniscus) stearnsii* Pilsbry, The Nautilus, vol. 4, p. 100.
 1891 *Patella grata* Gould, Pilsbry, Man. Conch., vol. 13, p. 135 (unfigured).
 1891 *Helcioniscus stearnsii* Pilsbry, Manual Conch., vol. 13, p. 132, pl. 48, figs. 16-18.
 1895 *Helcioniscus stearnsii* Pilsbry, Cat. Marine Moll. Japan, p. 112, pl. 7, figs. 4-6.
 1895 *Helcioniscus eucosmius* Pilsbry (non Pilsbry, 1891), Cat. Mar. Moll. Japan, p. 112, pl. 7, figs. 7-10.
 1959 *Cellana eucosmia* Pilsbry, Oyama & Takemura, Moll. Shells, vol. 3, *Cellana*, pl. 3, figs. 1-3.
 1959 *Cellana stearnsii* Pilsbry, Oyama & Takemura, Moll. Shells, vol. 3, *Cellana*, pl. 3, figs. 4-6.
 1961 *Patella grata* Gould, Johnson, Bull. 239, U. S. Nat. Mus. p. 86, pl. 19, figs. 1, 3 (lectotype).
 1962 *Cellana lucosmia* Pilsbry, Kira, Col. Illust. Shells of Japan, pl. 5, fig. 10.
 1962 *Cellana dorsuosa* forma *stearnsii* Pilsbry, Habe, Col. Illust. Shells of Japan, pl. 3, fig. 3.
 1967 *Cellana grata* Gould, Habe & Kosuge, Standard Book Jap. Shells in colour, pl. 3, figs. 4, 5.

Types—Lectotype of *grata*, selected by Johnson (1961), in the United States National Museum; USNM 1965. Type series of *stearnsii* in the Academy of Natural Sciences of Philadelphia.

Records—JAPAN: north shores of Nippon (lectotype of *grata*); Kii Province (types of *stearnsii*); Nagoya, Kii (AWBP coll.); Tosa (ANSP); Suwanosejima, Osumi (USNM); Kominato, Kazusa (AWBP coll.); Minojima (AWBP); Misaki (ANSP). KOREA: Matsushima Island (USNM).

Cellana mazatlandica (Sowerby, 1839)

(Pl. 67, figs. 17, 18; Pl. 135)

Range—Bonin Islands, Northwest Pacific Ocean.

Remarks—This very large but comparatively thin-shelled *Cellana* seems to be restricted to the Bonin Islands. It is easily recognised by its tall conical shape, with straight dorsal slopes, conspicuous spinose radial ribs, pale yellowish brown exterior, sparsely speckled with black, and rich chestnut-brown spatula, within.

Unfortunately the well known name for this striking member of the Japanese fauna, *nigrisquamata*, has to fall as a synonym of *Patella mazatlandica*, a misnomer, since the species does not occur in the tropical West American fauna. Also Pilsbry's *Patella (Helcioniscus) boninensis* is another synonym, being merely the adult of the species.

Description—Shell reaching a large size, up to 90 mm. (3½ inches) in length, solid but not massive, of moderate height to tall conical, with almost straight slopes; apex anterior third to sub-central. Sculpture of strong, sharply raised, prominently tubercled radial ribs; about 38 primary ribs and a varying number of secondary ribs, making a total of between 48 and 55. Colour of exterior pale yellowish brown, deepening towards the margin, the radials with scattered black spots;

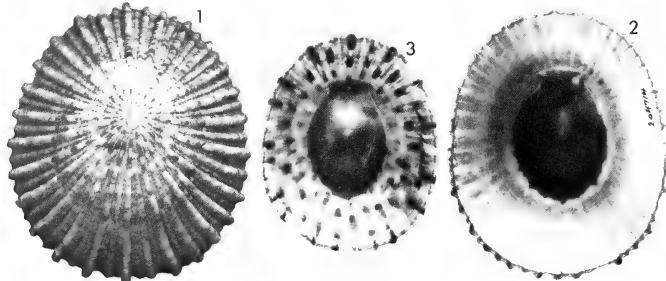


Plate 135. Figs. 1-3. *Cellana mazatlandica* (Sowerby, 1839). Chichu Jima, Bonin Islands, Japan. Fig. 1. 61 mm.; Fig. 2.

75 mm.; Fig. 3. 37 mm., AWBP coll. 204714 (better known as *boninensis* Pilsbry, 1891).

interior silvery-gray to cream, or pinkish white, with the spatula deep chestnut-brown, sometimes partly clouded with white callus; crenulated margin tinged with orange-brown.

Measurements (mm.) (all A.W.B. Powell coll.)—

length	width	height	
90.0	75.0	37.0	Bonin Islands
78.6	64.4	44.0	Bonin Islands
61.0	51.0	26.0	Bonin Islands
45.0	39.0	21.5	Bonin Islands

Synonymy—

- 1839 *Patella mazatlantica* Sowerby, Beechey's Voy. "Blossom", Zool. p. 148, pl. 39, fig. 12. "Mazatlan" in error.
 1854 *Patella nigrisquamata* Reeve, Conch. Icon. pl. 2, figs. 3 a, b. "Australia", in error.
 1891 *Patella (Helcioniscus) boninensis* Pilsbry, The Nautilus, p. 79. Bonin Islands.
 1891 *Helcioniscus boninensis* Pilsbry, Man. Conch. vol. 13, p. 131, pl. 66, figs. 1, 2; pl. 67, fig. 3.
 1891 *Helcioniscus nigrisquamatus* Reeve, Pilsbry, Man. Conch. vol. 13, p. 125, pl. 19, figs. 35, 36; pl. 48, figs. 13-15. (Concepcion, Chile", in error.
 1895 *Helcioniscus nigrisquamatus* Reeve, Pilsbry, Cat. Mar. Moll. Japan, p. 112, pl. 7, figs. 1, 2.
 1895 *Helcioniscus nigrisquamatus boninensis* Pilsbry, Cat. Mar. Moll. Japan, p. 112, pl. 7, fig. 3.
 1952 *Cellana nigrisquamata* Reeve, Kuroda and Habe, Check List Rec. Mar. Moll. Japan, p. 44.
 1959 *Cellana nigrisquamata* Reeve, Oyama and Takemura, The Moll. Shells, vol. 3, *Cellana*, pl. 3, figs. 9-12.

Records—BONIN ISLANDS: Ogasawara Island (ANSP); Chichi Jima (USNM).

Types—Three syntypes of *Patella nigrisquamata* Reeve, 1854, are in the British Museum (Natural History).

Cellana nigrolineata (Reeve, 1854)

(Pl. 67, figs. 15, 16; Pl. 137)

Range—Japan, common and widespread.

Remarks—This very attractive species is easily recognised by the orange-stained spatula and by the intricate external pattern of reddish brown

radial ribs and concentric growth lines on a greenish blue ground.

Description—Shell large, up to 78 mm. (3 inches) in length, but usually only about two-thirds that size, ovate, with an almost smooth margin, broadly rounded in profile, depressed to rather tall in fully-grown examples, with the apex varying between the anterior third and subcentral. Sculpture consisting of slightly raised, narrow radial ribs, crossed by weak concentric growth lines; between 50 and 60 radials, including intermediates, in fully adult shells. Colour distinctive; externally greenish blue, with the radial ribs and concentric growth lines picked out in reddish brown, or occasionally in black; internally, bluish silvery, with the external rib pattern showing through; spatula ivory-white but more or less stained orange-red, or sometimes dark-chocolate.

Measurements (mm.)—

length	width	height	
78.0	66.0	29.5	Chirigashima, Japan
58.0	53.5	16.5	Fukura Awaji, Japan
56.5	45.5	20.0	Chirigashima, Japan
48.5	36.5	13.0	syntype, British Museum
42.0	32.0	14.5	Nagasaki, Japan

Synonymy—

- 1854 *Patella nigro-lineata* Reeve, Conch. Iconica, pl. 18, figs. 43 a, b. "Island of Camiguin, Philippines", probably in error.
 1891 *Helcioniscus nigrolineatus* Reeve, Pilsbry, Man. Conch., vol. 13, p. 133, pl. 13, figs. 48, 49; pl. 14, figs. 71-74.
 1895 *Helcioniscus nigrolineatus* Reeve, Pilsbry, Cat. Mar. Moll. Japan, Detroit, p. 113.
 1952 *Cellana nigrolineata* Reeve, Kuroda and Habe, Check List Rec. Moll. Japan, p. 44.
 1959 *Cellana nigrolineata* Reeve, Oyama and Takemura, The Moll. Shells, vol. 3, *Patella-Cellana*, pl. 1, figs. 5, 6.
 1962 *Cellana nigrolineata* Reeve, Kira, Shells West. Pacific in Colour, p. 7, pl. 6, fig. 4.

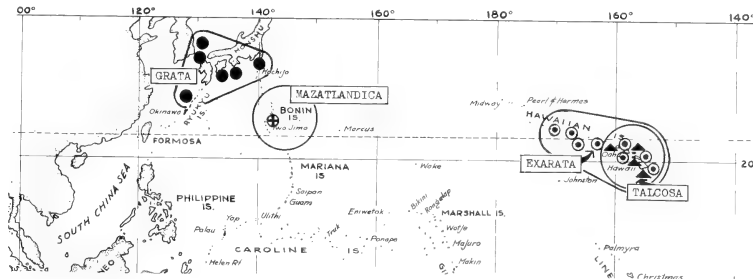


Plate 136. Geographical distribution of *Cellana grata* (Gould), *Cellana mazatlantica* (Sowerby), *Cellana exarata* (Reeve) and

Cellana talcosa (Gould).

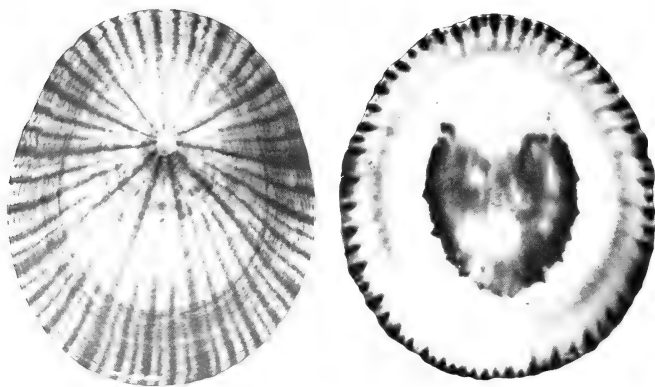


Plate 137. *Cellana nigrolineata* (Reeve, 1854), Chiringashima, Japan, 57.78 mm., AWBP coll. 52754.

Types—Four syntypes in the British Museum (Natural History), of which one, measuring 47.0 X 37.75 X 11.5 mm., is probably the one figured by Reeve, and this I now nominate as lectotype.

Records—"Philippines, Island of Camiguin"=Camiguin (type locality; probably in error); JAPAN: Hirado, Nagasaki Prefecture (Oyama and Takemura, 1959); Chiringashima (AWBP coll.); Fukura Awaji (USNM); Sagami Bay (Bishop Mus.); Manazutu (Auck. Mus.); Minoshima, Wakayama (AWBP coll.).

Cellana toreuma (Reeve, 1855)

(Pl. 138)

Range—Japan to Ryukyu Islands, Mariana Islands, Taiwan, Hongkong, China, and Philippines.

Remarks—There is little doubt that *toreuma* and *amussitata* represent extremes in sculptural development of a single species. Ino (1935, p. 31) has shown how size, rib-strength, outline, and other variations, can be accounted for by position in the tidal zone, nature of the substratum, and degree of exposure to wave stress.

The predominant form of the species is long and narrow with subparallel sides, and internally, the spatula is long and narrow also. Certain shells from the Philippines (Plate 71, figs. 7, 8)

are broadly ovate, but these are extreme individuals in populations that have narrow shells as well. Pilsbry's *Helcioniscus nigrolineatus* var. *divergens* is still another variant of *toreuma*, which is of large size, elongate-ovate, but with rounded rather than subparallel sides, and dense, fine, subgranose radial sculpture (Plate 71, fig. 6). Rugosely sculptured shells (Plate 71, fig. 3) are, according to Ino, found towards low water, where rocks have rough surfaces, contrasted with rock surfaces from higher levels that have been smoothed by erosion.

Description—Shell of moderate size, up to 40 mm. (1½ inches) in length, lightly built, very depressed, apex between the anterior third and fourth, elongate-ovate, narrow, with flattened sides, and tapered to a narrowly rounded front margin; margins weakly crenulated. Sculpture variable, typically consisting of 30-40 moderately strong, narrow, sharply raised primary radial cords, and from 1-3 secondary cords in each interspace, the whole crossed by fine sharp growth lines, that weakly decussate the radial cords, especially the secondary ones. Colour extremely variable; externally, usually greenish or buff, boldly rayed, mottled and blotched with dark reddish brown; internally bluish silvery, the external pattern showing through strongly; spatula ill defined, usually diffused chestnut-brown, but white callused at the anterior end.

Measurements (mm.)—

length	width	height	
40.0	31.0	9.0	Japan; Pilsbry, 1891, p. 135
39.5	28.5	5.8	Nagasaki
36.25	25.0	5.5	Waki, Satsuma

***Cellana exarata* (Reeve, 1854)**

(Pl. 67, figs. 4-6; Pl. 140)

Range—Hawaiian Islands.

Remarks—This well-known Hawaiian limpet is readily distinguished, when not in an eroded state, by its high-conical shape, with straight dorsal slopes, and black external ribbing, with narrow whitish interspaces. Internally the coloration is silvery to bluish leaden, and the clear-cut spatula is leaden to black, except when clouded with white callus.

Dr. Alison Kay (1969, pp. 1, 2) advocated separation of *exarata* into three distinct species, diagnosed as follows:—

- (1) *exarata*—Shell black, finely sculptured, the radial ribs not extending beyond the margin; foot of animal dark grey, mantle almost black; mantle appendages short, extending only 5 mm. beyond the edge of the shell. It belongs to the splash zone, on the islands of Oahu, Molokai, Maui and Hawaii.
- (2) *sandwichensis*—Shell black, coarsely sculptured, the radial ribs extending beyond the margin; foot of animal yellow, mantle grey;

mantle appendages long, some extending 20 mm. beyond the edge of the shell. It belongs to the low tidal zone, over the same range of localities where *exarata* is found.

- (3) *melanostoma*—Shell cream or white, with brown ribs; foot of animal and the mantle bright green. Outlying locations of the Hawaiian Chain, Necker, Nihoa, Lehua, Gardner Pinnacles and parts of Kauai.

After examining the excellent range of *exarata* material in the Bishop Museum, plus extensive material representative of the locations listed following, the writer is of the opinion that *sandwichensis* and *melanostoma*, so far as present evidence goes, do not qualify for higher status than ecotypes of *exarata*.

The juvenile stage, up to 24 mm. in length, in all three forms is identically tessellated in black and white, after which the radial ribs become continuously black, unless defaced by erosion. Most material from the outlying shoals and pinnacles of the Hawaiian Chain is subject to erosion, which reduces the surface of the adult shell to a uniform cream or white. However, in one lot from French Frigate Shoal, several

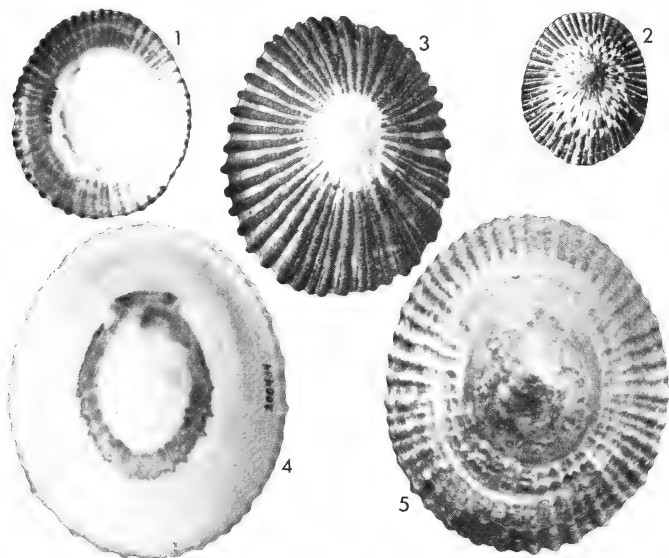


Plate 140. Figs. 1-5. *Cellana exarata* (Reeve, 1854), Hawaiian Islands. Figs. 1, 3. Kau Waiahukini, Hawaii. 47-53 mm., AWBP coll. 1958947. Fig. 2. Hilo, Hawaii, 35 mm., AWBP

coll. 195871. Figs. 4, 5. Gardner Pinnacles, 83 mm., AWBP coll. 200434.

adults have retained the black pigmented ribs right through to the fully adult shell.

Regarding differences in the coloration of the animal and in the relative lengths of the mantle appendages recorded by Dr. Kay, the writer has found similar variations in the New Zealand *Cellana radians*, which has a vertical range extending from low water to the lower edge of the splash zone. In the case of *exarata* versus *sandwichensis* it would be interesting to have observations upon limpet animals from mid-tidal locations.

The eroded *melanostoma* form of *exarata* is strikingly similar to *mazatlantica* of the Japanese Bonin Islands, and there is little doubt that there is near relationship. The Bonin species has a tessellated juvenile stage also, but the ribbing in the adult stage is tubercular and not continuously coloured, just sparsely speckled, and the apatula is deep chestnut-brown, not leaden to black, as it is in *exarata*.

Description—Shell reaching a large size, up to 83 mm. (3¼ inches) in length, but usually between 45 and 60 mm., solid, but not massive, narrowly ovate, with a subcentral nucleus, and conical with straight sides. Sculpture consisting of from 46 to 50 bold, sharply raised, flat-topped radials, that are smooth, except were crossed by weak concentric growth striae; margin shallowly corrugated to deeply indented by square-cut crenulations. Colour of exterior consisting of plain black radial ribs, with grey or whitish interstices, the apical area only, tessellated with black and

white dashes; internally silvery to bluish-lead, with the dark ribbing showing through; spatula leaden to solid black, but often partly or completely white callused. When the shell is eroded externally that surface becomes whitish or cream coloured, and the corresponding interior is usually diffused with yellow or orange-brown.

Measurements (mm.) (all AWBP coll.)—

length	width	height
83.0	68.5	40.0
70.0	58.0	34.0
64.0	55.5	37.5
42.0	32.0	12.0

Synonymy—

- 1839 *Patella exarata* Nuttall, in Jay, Cat. Shells, 3, p. 38 (nomen nudum). "Oregon, California," in error.
 1854 *Patella exarata* Reeve, Conch. Iconica, pl. 19, figs. 47 a, b.
 1854 *Patella undato-lirata* Reeve, Conch. Iconica, pl. 23, figs. 59 a, b. "Sandwich Islands."
 1860 *Patella sandwichensis* Pease, Proc. Zool. Soc., p. 437.
 1870 *Helcioniscus exaratus* Nuttall, Dall, Amer. Journ. Conch., vol. 6 (3), p. 279, pl. 16, fig. 29 (dentition).
 1891 *Helcioniscus exaratus* Nuttall, Pilsbry, Man. Conch., vol. 13, p. 126, pl. 47, figs. 1-3; 6-12.
 1891 *Helcioniscus melanostomus* Pilsbry, Man. Conch., vol. 13, p. 151, pl. 32, figs. 67-69.
 1969 *Cellana exarata*, *sandwichensis* and *melanostoma*: Kay, Hawaiian Shell News, vol. 17, no. 4, pp. 1, 2.

Types—Three syntypes in the British Museum (Natural History), of which, one measuring 42.5 x 35.0 x 18.0 mm. is evidently the one figured by Reeve and this I now nominate as lectotype.

Records—HAWAIIAN ISLANDS: OAHU: Haunama Bay; Manana Islands; Mokelea Rock; Kaena Point; Manana; Moku Manu; Popoia Islet. HAWAII: Hilo; Kona; Kau Waia-

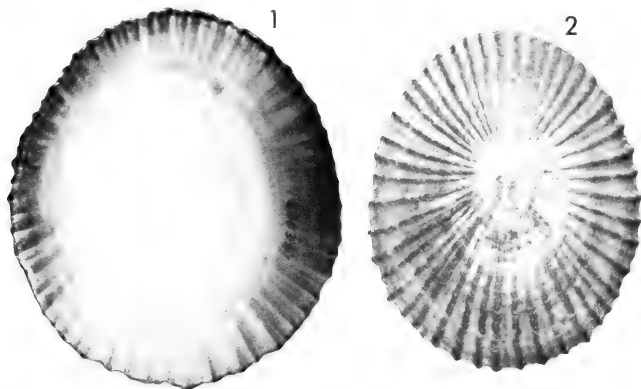


Plate 141. Figs. 1, 2. *Cellana talcosa* (Gould, 1846). Fig. 1. Molokai, Hawaiian Islands, 87 mm. AWBP coll. 195857. Fig. 2. Hawaiian Islands, 56.5 mm., AWBP coll. 22915

(better known under its preoccupied name, *argentata* Sowerby, 1839).

hukini. KAUAU: Haena. MAUI: West Honolulu. MOLOKAI: Kaunakakai (all Bishop Mus.). LA PEROUSE PINNACLE. (Tanager Exped., Bishop Mus.). GARDNER PINNACLES (Tanager Exped., Bishop Mus.). NECKER (Tanager Exped.). NIHOA (Tanager Exped. Bishop Mus.).

Cellana talcosa (Gould, 1846)

(Pl. 67, fig. 3; Pl. 141)

Range—Hawaiian Islands.

Remarks—This very large species of Hawaiian *Cellana*, long known as *Patella argentata* Sowerby, 1839, must take the name of *talcosa* Gould, 1846, owing to the prior *Patella argentata* Bosc, 1801.

Apart from large size, *talcosa* is distinguished by its nearly circular outline, broadly rounded, high-arched profile, very numerous, rather regular, radial ribs, and distinctive coloration, the exterior, when not encrusted, being reddish chestnut, and the interior silvery, with the scapula and surrounding muscle impression white. This species is found on exposed rocky shores and outer reefs near the low tide line.

Description—Shell solid, very large, up to 106 mm. (4½ inches) in length, broadly ovate, almost circular in outline, and roundly low-conical in profile, with the apex subcentral. Sculpture consisting of very numerous, narrowly rounded radial ribs, 58-76 primary, and a few secondary riblets in the interspaces of the lower half of the shell; margins finely crenulated. Colour, externally reddish chestnut, but almost invariably encrusted with algae and limy deposit; internally with a large ivory-white spatula, surrounded by a white callused area, and from there to the margin silvery, with the chestnut ribbing of the exterior showing through, especially towards the margin.

Measurements (mm.)—

length	width	height	
106.5	94.0	45.0	Kona, Hawaii
88.0	81.5	33.0	Molokai
87.0	81.0	37.5	Molokai

Synonymy—

- 1839 *Patella argentata* Sowerby in Beechey's Voy. "Blossom," Zool., p. 148, pl. 39, fig. 12 (non Bosc, 1801), "Valparaiso, Chile," in error.
 1846 *Patella talcosa* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 148. Hawaii, Sandwich Islands.
 1852 *Patella talcosa* Gould, U. S. Explor. Exped., Moll. p. 334, pl. 29, figs. 452 a, b.
 1854 *Patella cuprea* Reeve, Conch. Iconica, pl. 8, figs. 15 a, b., "Swan River," erroneous.
 1891 *Helcioniscus argentatus* Sowerby, Pilsbry, Man. Conch., vol. 13, p. 127, pl. 18, figs. 29, 30; pl. 65, fig. 93.
 1969 *Cellana talcosa* Gould, Kay, Hawaiian Shell News, vol. 17, no. 4, p. 1.

Types—The holotype of *talcosa* is in the United States National Museum, Washington (USNM. 5824).

Records—HAWAIIAN ISLANDS: HAWAII: South Point, Kauakae; Kona; Kau, Waikapuna; Puako. KAUAU: Koloa; MAUI: Hana; Honolulu; Keoneio (all Bishop Mus.). MOLOKAI: outer reefs (AWBP coll.). NIHOA (Bishop Mus.). There seem to be no Recent records of the species from the island of Oahu, but it occurs there fossil in raised coral reef formations.

Cellana taitensis (Röding, 1798)

(Pl. 75)

Range—Tahiti, Society Islands, and Pitcairn Island.

Remarks—This rather small-sized *Cellana* is lightly built, of ovate outline, moderately elevated, closely and rather regularly radially ribbed, and of dull greenish colour, maculated with numerous intermittent radial dark-brown lines and blotches. It is possibly closely allied to the Lord Howe Island *analogia* Iredale.

The writer is indebted to Dr. Harald A. Rehder of the National Museum of Natural History, Smithsonian Institution, Washington, for pointing out (personal communication) Röding's earlier name for the well known *tahitensis* (Pease). Röding's *Patella taitensis* was cited as coming from 'Othahaite' (= Tahiti), and was based upon Favanne, tab. 1, figs. N, N. Despite the crudeness of Favanne's illustrations, they suggest the common *Cellana* of Tahiti rather than *Patella* (*Scutellastra*) *flexuosa*, the only other patellid limpet known to occur in the Society Group.

Description—Shell small, 33.5 mm. (1¼ inches) in length, but usually smaller, of light build, broadly ovate, moderately elevated, and with the apex at about the anterior third; margin thin, minutely crenulated. Sculpture consisting of very

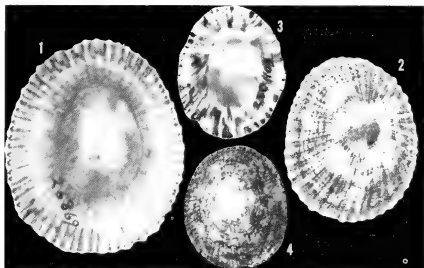


Plate 142. Figs. 1-4. *Cellana taitensis* (Röding, 1798). Figs. 1, 2. Pitcairn Island, 25-30 mm., AWBP coll. 26869. Figs. 3, 4. Tautira, Tahiti, 24-25 mm., AWBP coll. 250703.

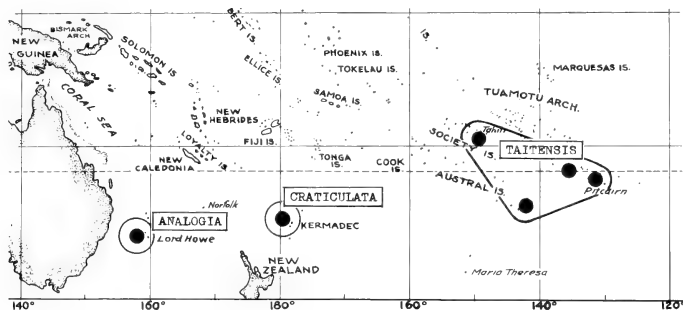


Plate 143. Geographical distribution of *Cellana analogia* Iredale, *Cellana craticulata* (Suter) and *Cellana taitensis* (Röding).

numerous, moderately strong, narrow, radial riblets that are deeply cut by closely-spaced concentric growth lines, resulting in nodulation, especially towards the margin. Colour: externally, varying from dull greenish to greenish white, with a variable radiate pattern in dark-brown, ranging from intermittent radial lines to bold blotches; internally, iridescent dull dark bluish grey, the terminal points of the external ribbing forming a narrow dark border; spatula dark greyish or greenish brown, sometimes clouded with white callus.

Measurements (mm.).—

length	width	height	
33.5	27.00	11.50	Tautira, Tahiti
29.0	25.00	14.00	Pitcairn
26.0	21.75	8.75	Tautira, Tahiti
18.0	15.00	6.00	Tautira, Tahiti



Synonymy—

- 1798 *Patella taitensis* Röding, Mus. Bolten., pt. 2, p. 7, sp. 68. Based upon Favanne, tab. 1, figs. N. N.
 1868 *Tectura taitensis* Pease, Amer. Journ. Conch., vol. 4 (3), p. 98, pl. 11, fig. 21.
 1891 *Helcioniscus taitensis* Pease, Pilsbry, Man. Conch., vol. 13, p. 129, pl. 67, figs. 4-8.
 1907 *Patella (Helcioniscus) taitensis* Pease, Couturier, J. de Conchyl., vol. 55 (2), p. 173. (Pitcairn Island).
 1966 *Cellana taitensis* Pease, Rehder, Hawaiian Shell News, vol. 14 (8), p. 5. Pitcairn Island.

Records—TAHITI (type locality): S. W. of Tautira, on basalt rocks in the splash zone (R. Robertson, 22 July, 1952; ANSP.). PITCAIRN ISLAND (AWBP coll.): Bounty Bay (Rehder, 1966). TUAMOTU ARCHIPELAGO: Mangareva (Aust. Mus.).

Cellana ardosiaea
(Hombron and Jacquinot, 1841)

(Pl. 73, figs. 7, 8; Pl. 144)

Range—Island of Juan Fernandez, off the coast of Chile.

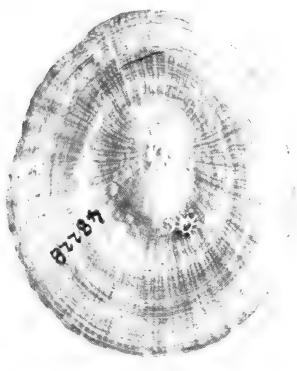


Plate 144. *Cellana ardosiaea* (Hombron & Jacquinot, 1841), Island of Juan Fernandez, off Chile, 46-58 mm., AWBP

coll. 48228.

Remarks—This is the furthest east yet recorded for the Indo-Pacific genus *Cellana*. Pilsbry (1891) considered *ardosiaea* to be allied to the Society Islands *taitensis*, but that is a most unlikely relationship. From all other species of *Cellana*, the Juan Fernandez shell stands apart, with its nearly circular, spreading form with its straight dorsal slopes, high conical profile, and its small, erect, nearly central apex.

Unfortunately the writer has no preserved animals of *ardosiaea*, but reference to Schuster (1913) and to Thiem (1917), respectively, leave no doubt that the species is a *Cellana*, not a *Nacella* (*Patinigera*), which latter relationship one would have expected, owing to the geographical proximity of *ardosiaea* to the South American mainland.

The epipodial fringe, so characteristic of *Nacella* and its subgenus *Patinigera*, is absent in *ardosiaea*, as also is any trace of the equally characteristic bronzy coloration of the shell.

Thiem (1917, p. 389) described in *ardosiaea* a presumed sensory organ, the "vorderer subpalliatr Sinnestreif" (anterior subpallial sensory stripe), and a longer posterior one, the former evidently the same structure as Fretter and Graham's (1962, p. 118) "lateral glandular streak" in *Patella*. The anterior sensory stripe, or lateral glandular streak, was noted in several species of *Cellana*, but not the 'posterior stripe,'

which possibly, could have resulted from contraction during preservation.

Description—Shell moderately large, up to 58 mm. (2½ inches) in length, rather solid, broadly ovate, with the small erect apex nearly central; tall-conical with the sides descending almost perfectly straight; margin smooth to weakly crenulated. Sculpture consisting of weak, evenly-spaced, radial primary cords, with 3-4 secondary cords or threads in each interspace, the whole crossed by numerous concentric growth threads. Colour of exterior light bluish olive, darker towards the margin; the apex yellowish to reddish brown; interior silvery bluish grey, except for the spatula, which is yellowish to orange-brown, and there is a narrow rim of greenish olive at the margin.

Radula—The radula, as figured by Schuster (1913, p. 304, text fig. V), is not diagnostic, since there is no basic difference between the radula of *Cellana* and that of the *Nacella* group.

Measurements (mm.)—

length	width	height	
57.5	51.5	23.0	all Juan
57.5	52.0	21.5	Fernandez
55.0	46.0	20.5	Island
46.0	39.0	17.0	
37.0	32.5	14.5	

Synonymy—

- 1841 *Patella ardosiaea* Hombron & Jacquinot, Ann. Soc. Nat., vol. 2 (16), p. 190.
 1854 *Patella clathratula* Reeve, Conch. Iconica, pl. 14, figs. 30 a, b.
 1891 *Helcioniscus ardosiaeus* H. and J., Pilsbry, Man. Conch., vol. 13, p. 124, pl. 32, figs. 63-66.
 1913 *Helcioniscus ardosiaeus* H. and J., Schuster, Zool. Jahrb., Jena, Suppl. 13, pp. 281-384.
 1917 *Helcioniscus ardosiaeus* H. and J., Thiem, Zool. Naturw., vol. 54, pp. 333-404.

Records—JUAN FERNANDEZ: (Stearns coll., USNM ANSP).

Cellana conciliata Iredale, 1940

(Pl. 145; Pl. 148, fig. 3)

Range—North Queensland down to Bargara, South Queensland.

Remarks—This species is easily distinguished from *tramoserica* by its very fine and dense radial sculpture, and in the adult stage by a disproportionate broadening of the posterior end. Also the radula differs from that of *tramoserica* in that all the teeth are shorter and rather stouter.

Description—Shell of moderate size, up to 40 mm. (1½ inches) in length, broadly ovate, with very weakly scalloped edges, and rather low in

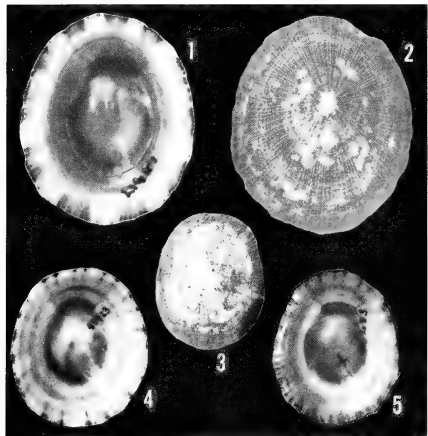


Plate 145. Figs. 1-5. *Cellana conciliata* Iredale, 1940. Figs. 1, 2. Lammernore Heads, Keppel Bay, Queensland, 35-38 mm., AWBP coll. 45417. Figs. 3-5. Keppel Bay, Queensland, 34-39 mm. (Fig. 5, marked X, compared with holotype), AWBP coll. 45423.

height, with the apex subcentral. Sculpture delicate and rather even, consisting of very numerous radial riblets, due to little difference in strength between primaries and secondaries; about 140 riblets in all. As the shell reaches mature size, it tends to gain little height but spreads posteriorly. Concentric growth lines are weak and apparent only at the margin in adults. Colour greenish or bluish grey externally, often broadly or narrowly radially banded in dark brown, with pale chestnut lines in the interstices; young shells often uniformly dark greenish grey; silvery-blue to creamy-white within, sparsely and faintly rayed with bluish grey towards the margin; spatula fawn to dark yellowish brown, often clouded with a white callus in mature shells.

Radula—Similar to that of *tramoserica* but all the teeth are shorter and stouter than in that species (Macpherson, 1955, p. 239).

Measurements (mm.)—

length	width	height	
44.0	39.0	15.0	Keppel Bay; paratype
40.0	34.0	14.0	Keppel Bay; holotype
38.7	34.0	15.0	Keppel Bay; topotype
33.0	28.0	14.5	Keppel Bay; topotype

Synonymy—

1940 *Cellana conciliata* Iredale, Aust. Zool. 9, p. 432, pl. 33, figs. 1-3, 19, 20.

1955 *Cellana conciliata*: Macpherson, Proc. Roy. Soc. Vict., vol. 67 (2), p. 238, pl. 10, figs. 1, 2.

Types—Holotype and paratypes in the Australian Museum, Sydney; paratypes and topotypes in Powell collection, Auckland.

Records—QUEENSLAND: Keppel Bay (type locality); Bargara, near Bundaberg (Mrs. J. Kerslake; AWBP coll.).

***Cellana turbator* Iredale, 1940**

(Pl. 146, figs. 5-7; Pl. 148, fig. 4)

Range—Caloundra, south Queensland.

Remarks—This is a small conical species that differs from the young forms of *tramoserica* in sculpture, the radial ribbing being coarsely nodulose, in coloration, and also in the radula, as described below.

Description—Shell small, up to 18 mm. (¾ inch) in length, regularly ovate, with an elevated, roundly-conical, profile; apex at the anterior third. Sculpture bold, consisting of about 25 nodulose, primary, radial ribs, with a single secondary radial, almost as strong, in each interspace; margin weakly crenulated. Colour, green-

ish white externally, and creamy, pinkish, or silvery-white within; sparsely and intermittently lined and speckled with dark-brown; spatula dark chestnut, with clear outlines, or diffused with callus.

Radula—Formula 3+1+(10+1)+1+3. The radula is distinctive; the two central teeth are sharply pointed but have a small spur on the outer edge; the bicuspid laterals have a long inner cusp, with a prominent notch about one fourth of the way down from the tip, and a blunt conical basal cusp, rising to a third the height of the main cusp; marginals three, long and slender, the outer one the largest (Macpherson, 1955, p. 238).

Measurements (mm.)—

length	width	height	
20.0	15.5	7.0	Caloundra
18.0	14.7	5.8	Caloundra
15.0	12.0	6.0	holotype
14.5	12.0	5.0	Caloundra

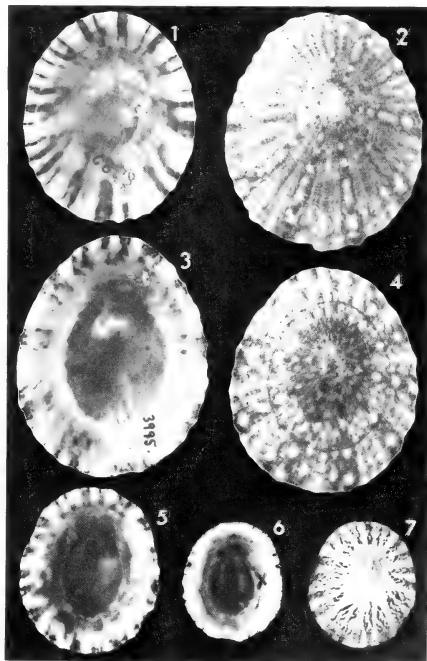


Plate 146. Figs. 1-4. *Cellana tramoserica* (Holtz, 1802) Figs. 1, 2. Manly, New South Wales, 34 mm., AWBP coll. 3965. Figs. 5-7. *Cellana turbator* Iredale, 1940. Caloundra, Queensland, 14.5–20 mm. (One marked X, compared with holotype), AWBP coll. 45440.

Synonymy—

1940 *Cellana turbator* Iredale, Aust. Zool., vol. 9, p. 433, pl. 32, figs. 16-18.

1955 *Cellana turbator*: Macpherson, Proc. Roy. Soc. Victoria, vol. 67 (2), p. 239, pl. 10, figs. 3, 4.

Types—Holotype and paratypes in the Australian Museum, Sydney.

Records—Known only from the type locality, Caloundra, Queensland.

***Cellana tramoserica* (Holten, 1802)**

(Pl. 73, figs. 1-3; Pls. 146-148)

Range—South Australia, Victoria, east coast of Tasmania, New South Wales and southern Queensland.

Remarks—This species is distinguished from *solida* by the more numerous, subcarinate, linear-spaced ribs, and resultant finer marginal crenulations, the variegated colour pattern, smaller adult size, and lesser solidity. The various colour forms are described below. Iredale's *sontica* from Caloundra, South Queensland, is a small rather drab-coloured form of the species, that does not merit separation. Dr. Hope Macpherson (1955, p. 238) remarked that a series covering both typical *tramoserica* and *sontica* showed that there were no radular differences between the two forms.

Description—Shell moderately large, up to 60 mm. (2½ inches) in length, broadly ovate, roundly conical with the apex subcentral, and with a finely scalloped margin. Sculpture consisting of about 36 strong, subcarinate radial ribs with narrow interstices, the whole crossed by dense, fine, sharp growth lines. Colour exceedingly variable: externally yellowish, pink, or light-brown, with some of the primary ribs dark-fawn, or chocolate, either plain or with elongated whitish patches; again, some of the ribs may be reddish, and in others the rib interstices only may be lined in dark-brown; internally the shell is often yellowish to orange, or golden nacreous, with the spatula varying from dark-fawn to a whitish callus; the margin is variously radially lined by the dark, external ribbing showing through the thinner outer edge.

Radula—Formula 3 + 1 + (1+0+1) + 1 + 3. The pair of central teeth are long, curved and unicuspid, as in *solida*, but the pair of bicuspid laterals have a distinct notch, half way down from the tip, and there is a small conical cusp at

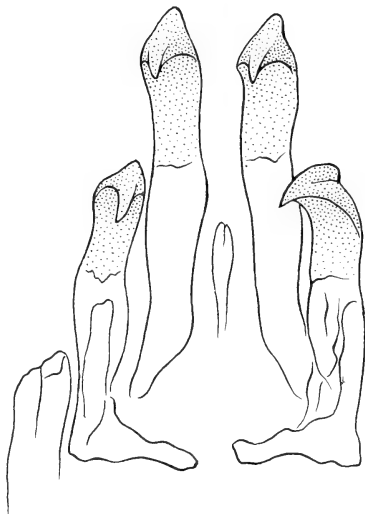


Plate 147. *Cellana tramoserica* (Holten), Alan Bay, Great Australian Bight, South Australia. Radula.

the base; of the three marginal teeth, the outer two are sharply pointed, but the inner one has the tip bent over slightly to form a blunt cutting point (Macpherson, 1955, p. 239). It is of interest that a radula from a specimen taken at Alan Bay, Great Australian Bight was four times the length of the shell.

Measurements (mm.)—

length	width	height	
59.5	48.0	28.0	Noosa Head, Queensland
54.0	46.0	24.0	Mainly, New South Wales
37.0	31.0	16.0	Long Reef, New South Wales
22.5	19.0	6.0	The Spit, Port Jackson, N.S.W.

Synonymy—

1802 *Patella tramoserica* Holten, Enum. Syst. Conch., Chemnitz, p. 85 (based upon Chemnitz, Conch. Cab., vol. 11, pl. 197, figs. 1912, 1913.)

1825 *Patella variegata* Blainville, Dict. Sci. Nat., vol. 38, p. 100.

1825 *Patella tramoserica* Martyn, Sowerby, Cat. Tankerville Coll., p. 30.

1831 *Patella jacksoniensis* Lesson, Voy. "Coquille" Zool., vol. 2 (1), p. 418.

1854 *Patella tramoserica* Martyn, Reeve, Conch. Iconica, pl. 13, figs. 27 a-c.

1891 *Helcioniscus tramoserica* Martyn, Pilsbry, Man. Conch., vol. 13, p. 142, pl. 70, figs. 49, 52.

1924 *Cellana variegata ariel* Iredale, Proc. Linn. Soc. N.S.W., vol. 49, p. 242.

1940 *Cellana sontica* Iredale, Aust. Zool., vol. 9, p. 433, pl. 33, figs. 10-12.

1955 *Cellana tramoserica* Holten, Macpherson, Proc. Roy. Soc. Victoria, vol. 67 (2), p. 237.

Records—SOUTH AUSTRALIA: Alan Bay, Great Australian Bight (I. G. Marrow); Aldinga (AWBP coll.). VICTORIA: St. Kilda; Mornington; Point Nepean (Macpherson, 1955); Port Fairy (type of *ariel*). TASMANIA: east coast, rare and small (W. L. May, 1923). NEW SOUTH WALES: Botany Bay (type locality); Long Reef; Manly; The Spit, Port Jackson; Shellharbour. QUEENSLAND: Port Douglas; Point Vernon (Mrs. J. Kerslake; AWBP coll.); Noosa Head; Stradbroke Island; Caloundra (type of *sontica*); near Brisbane (all AWBP coll.).

Cellana solida (Blainville, 1825)

(Pl. 73, figs. 4-6; Pl. 148, fig. 1; Pl. 150)

Range—Tasmania, Bass Strait Islands, and Victoria to eastern South Australia, in the algal zone of the lower littoral.

Remarks—This is a large solid limpet, sculptured with bold, rounded, radial ribs. Blainville's *solida* applies to the smaller size range of the species, and his *rubraurantiaca* to the fully adult in which the internal colour usually deepens to orange-red at the margin. A conspicuous feature

of this species is the clearly defined dark-coloured spatula, which varies from olive-brown to greenish or bluish slate.

Description—Shell large, up to 79 mm. (over 3 inches) in length, solid, broadly ovate, with a deeply scalloped margin, tall conical, with the apex varying between subcentral and the anterior third. There are about 26 strong, rounded, radial ribs, crossed by dense, sharp-edged growth lines. Colour variable with age; young shells are grey or greenish grey within, the spatula clearly defined, olive to bluish slate; becoming yellowish, and finally pale orange at the margin, where bold radiate dark red-brown radials show through the shell substance; exterior dull grey to pinkish buff, often with radiate yellowish brown streaks in the rib interstices. Fully grown examples tend to have the spatula more or less masked by a thick whitish callus, and the margin is bright reddish orange, regularly banded by the reddish brown radials. In this latter form, *rubraurantiaca*, the exterior is pinkish white.

Radula—Formula $3 + 1 + (1+0+1) + 1 + 3$. The two centrals are long, slender, curved and unicuspid; the pair of laterals are bicuspid, the main member similar to the centrals, but with a small additional cusp at the base; the three marginals are narrow and slender, the inner one curved over at the top into a cutting edge, the other two simple (Macpherson, 1955, p. 236).

Measurements (mm.)—

length	width	height	
78.5	67.0	38.0	Bass Strait
75.0	62.0	31.0	St. Helens, Tasmania
74.0	61.5	33.0	South Australia
51.0	43.5	19.5	St. Francis Id., S. Australia

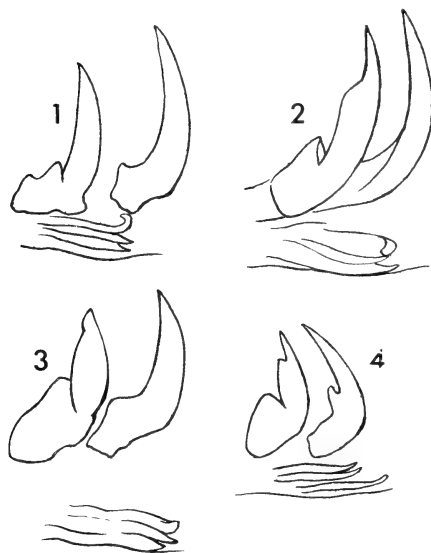


Plate 148. Radulae of Australian *Cellana* in profile: lateral tooth (left) and central tooth (right). Fig. 1, *Cellana solida* (Blainville). Fig. 2, *Cellana tramoserica* (Holten). Fig. 3, *Cellana conciliata* Iredale. Fig. 4, *Cellana turbator* Iredale. All from Macpherson, 1955, Proc. Roy. Soc. Victoria, vol. 67, pp. 236, 238, 239 and 240.

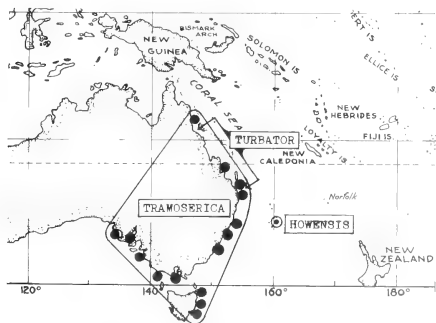


Plate 149. Geographical distribution of *Cellana tramoserica* (Holten), *Cellana turbator* Iredale and *Cellana howensis* Iredale.

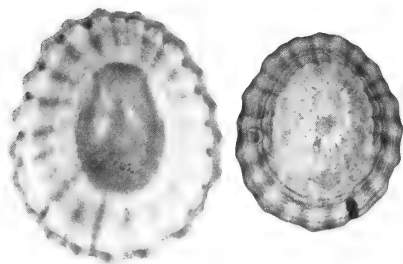


Plate 150. *Cellana solida* (Blainville, 1825), Corny Point, South Australia, 51 and 42 mm., AWBP coll. 187.

Synonymy—

- 1825 *Patella solida* Blainville, Dict. Sci. Nat., vol. 38, p. 110.
 1825 *Patella rubraurantiaca* Blainville, Dict. Sci. Nat., vol. 38, p. 111.
 1849 *Patella limbata* Philippi (non Röding, 1798), Abbild. und Besch. Conch., vol. 3 (6), p. 71.
 1854 *Patella limbata* Philippi, Reeve, Conch. Iconica, pl. 13, figs. 29 a, b.
 1891 *Helcioniscus limbata* Philippi, Pilsbry, Man. Conch., vol. 13, p. 143, pl. 71, figs. 53-56; pl. 17, figs. 28, 29.
 1955 *Cellana solida* Blainville, Macpherson, Proc. Roy. Soc. Victoria, vol. 67 (2), p. 236.
 1962 *Cellana solida* Blainville, Macpherson and Gabriel, Mar. Moll. Victoria, p. 45.

Records—TASMANIA: Port Arthur (AWBP coll.); Circular Head (AWBP coll.); Penguin (A. F. B. Hull; AWBP coll.); William's Island, Bass Strait. VICTORIA: Cape Otway; Wilson's Promontory (Macpherson, 1962, p. 47). SOUTH AUSTRALIA: Point Sinclair (AWBP coll.); St. Francis Island (AWBP coll.); Corny Point (AWBP coll.).

?*Cellana carpentariana* Skwarko, 1966

(Pl. 152, fig. 1)

Range—Australia, Mount Young, Northern Territory, late Neocomian, lower Cretaceous.

Remarks—This species bears some resemblance to the Recent *enneagona* Reeve, 1854 and the Australian lower Miocene *cudmorei* Chapman and Gabriel, 1923. If *carpentariana* is really a *Cellana* then it is the earliest known member of the genus.

Description—(original) "The shell is moderately large and inflated. Its apex is obtusely pointed, situated anteriorly, and not incurved. The slopes are straight in the front and on the sides of the shell but convex on the posterior wall, with a wavy posterior margin. The posterior slope is ornamented with four primary, three secondary, and six tertiary straight radial ribs which gradually increase in breadth away from the umbo. The primary ribs are straight, sharp-crested, and prominent. Radial ribbing is also

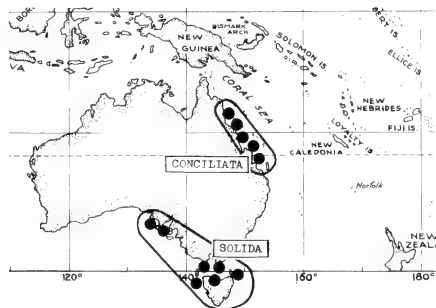


Plate 151. Geographical distribution of *Cellana conciliata* Iredale and *Cellana solida* (Blainville).

present on the sides, and on the anterior end of the shell, but is not distinct and the costae there seem to belong to one order only. Ribs are crossed by irregular growth-rugae and somewhat more irregular growth striae".

Measurements—No size indicated other than "moderately large."

Synonymy—

- 1966 *Cellana* (?) *carpentariana* Skwarko, Comm. Aust. Dept. Nat. Dev. Bur. Min. Res. Geol. and Geophys. Bull. 73, p. 120, pl. 14, fig. 11.

Cellana cudmorei Chapman and Gabriel, 1923

(Pl. 152, fig. 2)

Range—Australia, polyzoal rock of Batesford, near Geelong, Victoria, Batesfordian Stage, lower Miocene.

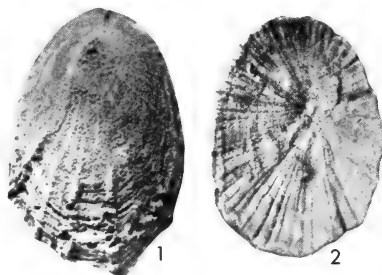


Plate 152. Fig. 1. ?*Cellana carpentariana* Skwarko, 1966, late Neocomian, lower Cretaceous, Mt. Young, Northern Territory, Australia. Holotype, from Skwarko, 1966, pl. 14, fig. 11. Fig. 2. *Cellana cudmorei* Chapman & Gabriel, 1923, Batesford, Victoria, Australia, lower Miocene; 40 mm. Holotype, from Chapman & Gabriel, 1923, pl. 1, fig. 1.

Remarks—Chapman and Gabriel considered this species to be ancestral to *tramoserica*, but it is not related to that species, being in fact a member of the *radiata* series, as shown by the nine broad primary rays, a very similar Recent shell being *radiata* subspecies *enneagona* Reeve, 1854, with its synonym *articulata* Reeve, 1855, the latter from the Philippines. Similar shells range northward to the Bonin Islands, Japan. This tendency to develop nine primary rays occurs sporadically throughout the *radiata* series.

Description—(original) "Shell large, elevated, oval, rather strongly built; apex situated about one-third from the anterior margin. Sculpture consisting of numerous strong riblets, with two or three smaller one occupying the interspaces. Growth-lines undulate, fine, not well developed."

Measurements (mm.)—

length	width	height
40.0	30.0	10.0

holotype

Synonymy—

1923 *Cellana cudmorei* Chapman and Gabriel, Proc. Roy. Soc. Vict., new ser., vol. 36, p. 23, pl. 1, fig. 1.

Types—The holotype is in the National Museum of Victoria.

Cellana hentyi Chapman and Gabriel, 1923

Range—Australia, shell bed at Forsyth's, Grange Burn, near Hamilton, Victoria, Kalimnan Stage, lower Pliocene.

Remarks—Chapman and Gabriel compared their species firstly with *Patella peronii* (as *squamifera*) and then as an alternative with *Cellana tramoserica* (as *variegata*). However the latter interpretation is the more likely one, the sculpture being similar to that in the Recent *tramoserica*, except that the concentric lines produce knotted nodes where they cross the radials. The original illustration is too indistinct to copy.

Description—(original) "Shell of medium size, elevated, narrowly oval, apex a little in front of centre. In the present state of fossilisation the apex is denuded of ornament. Surface ornament consisting of moderately strong radiating ribs, with several intermediate, less pronounced riblets; these are crossed by growthlines which are strongly undulate and which are produced at the intersections into nodulose growths. Shell still retaining its natural colour, from olive green to black".

Measurements (mm.)—

length	width	height
20.0	14.5	10.5

holotype

Synonymy—

1923 *Cellana hentyi* Chapman and Gabriel, Proc. Roy. Soc. Vict., new ser., vol. 36, p. 23, pl. 1, fig. 2.

Types—The holotype is in the National Museum of Victoria.

Cellana analogia Iredale, 1940

(Pl. 153, figs. 4-6)

Range—Lord Howe Island, Roach Islands

Remarks—This species is distinguished from *howensis*, another Lord Howe Island species, mainly in the form of the sculpture, the differences being especially marked when young shells of each are compared. The sculpture in *analogia* consists of coarse sharply carinated radials that are rendered scabrous to nodulose by dense concentric growth ridges, but in *howensis* the radials are flattened, have linear interspaces, and weaker concentric sculpture renders the radials only slightly granulose over the earlier growth stages, the ribbing becoming smooth towards the margin in the adult.

Description—Shell of moderate size, up to 41 mm. (1½ inches) in length, solid, broadly ovate, only moderately elevated, the apex varying from subcentral to the anterior third; margin strongly

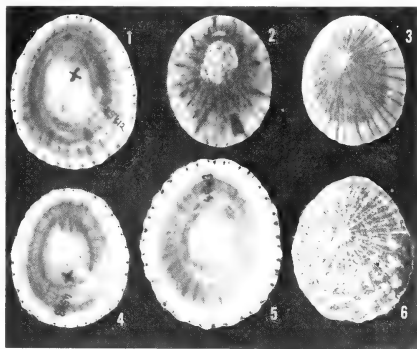


Plate 153. Figs. 1-3. *Cellana howensis* Iredale, 1940, Lord Howe Island, 30-32 mm., AWBP coll. 45142 (one marked X compared with holotype). Figs. 4-6. *Cellana analogia* Iredale, 1940, Lord Howe Island, 32-39 mm., AWBP coll. 45143 (one marked X compared with holotype).

crenulated. Sculpture strong and coarse, consisting of numerous carinated radials; primaries more or less alternating with secondaries; linear interspaces deep, and the whole surface rendered strongly scabrous to nodulose by dense concentric growth ridges. Young examples are very depressed and have 9 of the primary radials somewhat stronger than the rest. Colour of exterior dull-white; interior greyish white, the spatula yellowish to fawn, but mostly completely covered by white callus; margin white-callused, with short dark-brown lines corresponding to the external rib interstices; in some examples these radial colour lines extend intermittently, within the shell substance, almost to the spatula.

Measurements (mm.)—

length	width	height	
41.0	36.7	20.0	Lord Howe Id.
39.0	33.0	13.0	Lord Howe Id.
37.0	31.0	17.0	holotype
33.5	28.5	10.0	Lord Howe Id.

Synonymy—

1940 *Cellana analogia* Iredale, Aust. Zool., vol. 9 (4), p. 432, pl. 32, figs. 2, 14; pl. 33, figs. 7-9.

Types—The holotype and paratypes are in the Australian Museum, Sydney, and there is a series of topotypes in the Powell collection, Auckland.

***Cellana howensis* Iredale, 1940**

(Pl. 153, figs. 1-3)

Range—Lord Howe Island, Ned's Beach.

Remarks—This species is distinguished from the other Lord Howe Island limpet, *C. analogia*, in the form of the ribbing which consists of broad low radials that are separated by linear interspaces. There is also, a radial pattern of dark-brown lines in the rib interstices, as well as varying radial streaks of the same colour. The nearest related species seems to be the Australian *tramoserica*.

Description—Shell of moderate size, up to 34 mm. (1½ inches) in length, rather solid, ovate, elevated, the apex at the anterior fourth; margin finely crenulated. Sculpture consisting of numerous, flattened, radial ribs of varying width, some rather broad, and all with linear interspaces; these radials are further subdivided by one or two shallower radial grooves, and the whole surface is densely and delicately concentrically crossed by growth lines that render the radials weakly granulose over the early part of the shell; there being a general smoothness of the

ribbing towards the margin. Colour of exterior greenish grey to greyish buff, the narrow interspaces lined in dark-brown, and some have radial streaks of the same colour; interior yellowish to orange-brown, with the spatula dark reddish brown, usually more or less completely clouded with greyish-white callus; the external pattern shows through strongly except in fully adult examples, which have a rounded callused margin, and in these the external radial lines form short radial dashes corresponding to the external linear interspaces.

Measurements (mm.)—

length	width	height	
34.0	28.0	13.25	Lord Howe Id.
31.5	26.5	13.50	holotype
31.0	26.0	18.00	Lord Howe Id.
26.0	21.0	11.50	Lord Howe Id.

Synonymy—

1940 *Cellana howensis* Iredale, Aust. Zool., vol. 9 (4), p. 432, pl. 32, figs. 1, 13; pl. 33, figs. 4-6.

Types—The holotype and paratypes are in the Australian Museum, Sydney, and there is a series of topotypes in the Powell collection, Auckland.

***Cellana craticulata* (Suter, 1905)**

(Pl. 154, 155; Pl. 156, fig. 2)

Range—Kermadec Islands.

Remarks—This is a difficult species to describe in general terms, since it is excessively variable, assuming different shapes, sizes, sculptural developments and colour patterns, presumably in relation to degrees of exposure, and vertical distribution within the tidal belt. This complex was divided by Oliver (1915, pp. 511-514) into 4 species and 2 subspecies, but his interpretation breaks down in practice, as evidenced by Oliver's own qualifying remarks (l.c. p. 511):—"examination of ample material leads one to the conclusion that in the Kermadec group there exist about four species of *Cellana* in the process of being formed out of a single species, and the young of all are frequently so much alike that a satisfactory disposition is scarcely possible."

Another significant point is that although three of the named forms have their respective type localities elsewhere in the group than Raoul Island, all six are recorded from that island. Lives on rocks from low to high water.

Description—Shell of small to moderately large size, from 21.5 to 50.6 mm. (¾-2 inches) in length,

narrowly to broadly ovate, depressed to elevated, with weakly crenulated to strongly corrugated margins, and excessively variable sculpture and colour pattern. The typical form is elongate oval, depressed, and strongly sculptured, the radials basically in the form of distant, broadly rounded corrugations, these and the interspaces, densely overridden by narrow radial cords, which are rendered weakly nodulose by dense concentric growth lines. Coloration; externally, olive with most of the radial folds broadly radially streaked in dark-brown to black; internally, silvery with the radiate external pattern showing through,

strongest at the margin; spatula long and narrow, dark-sepia, clouded with white callus. The form *hedleyi* has the radial folds well developed but the outline is more broadly ovate; *corrugata* is similar but has maximum development of the radial folds; *vulcanica* is high-conic and coarsely ribbed but without radial folds; *scopulina* is rounded and high-conic also, but the radial sculpture is not prominent, only occasional young examples have the radial folds, and the general coloration is yellowish to pinkish orange, often with radiate streaks and interstitial dark-brown lines.

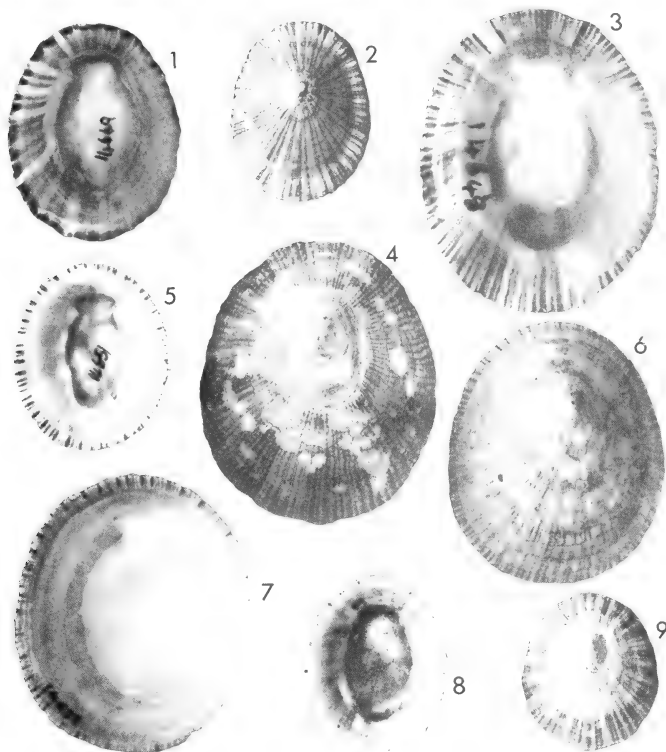


Plate 154. Figs. 1-9. *Cellana craticulata* (Suter, 1905), Kermadec Islands. Figs. 1, 2. Raoul Island (typical form), 26-30 mm., MF14649. Figs. 3, 4. Raoul Island (*prolixa* form), 35 mm., MF14648. Fig. 5. Denham Bay, Raoul Island (*prolixa* form), 29 mm., MF14651. Figs. 6, 7. French Rock (*scopulina*

form), 50 mm., MF14658. Figs. 8, 9. Raoul Island, (*scopulina* form), 21-22 mm., AWBP coll. (The MF numbers of this and the following plate refer to Dominion Museum, Wellington specimens in the W. R. B. Oliver collection; Oliver's determinations in brackets).

Measurements (mm.)—

length	width	height	
50.0	42.0	20.8	<i>scopulina</i> form; Oliver, 1915
45.8	37.5	14.2	<i>hedleyi</i> form; Oliver, 1915
42.8	37.0	11.3	<i>corrugata</i> form; Oliver, 1915
39.0	30.5	9.5	<i>hedleyi</i> form; Raoul Id.
32.2	28.0	16.3	<i>vulcanica</i> form; Oliver, 1915
31.4	26.4	7.4	<i>prolixa</i> form; Oliver, 1915
26.5	23.0	7.5	<i>scopulina</i> form; Raoul Id.
25.0	20.0	7.0	holotype of <i>craticulata</i>

Synonymy—

1905 *Helcioniscus craticulatus* Suter, Proc. Malac. Soc., Lond., vol. 6, p. 352, text figs.

- 1910 *Helcioniscus dirus* Reeve, (non Reeve, 1855) Iredale, Proc. Malac. Soc., Lond., vol. 9, p. 71.
 1910 *Helcioniscus craticulatus* Suter, Iredale, Proc. Malac. Soc., Lond., vol. 9, p. 72.
 1913 *Helcioniscus antipodum* Smith, (non E. A. Smith, 1874) Suter, Man. N. Z. Moll., p. 79 (in part).
 1915 *Cellana craticulatus* Suter, Oliver, Trans. N. Z. Inst., vol. 47, p. 511.
 1915 *Cellana craticulatus prolixus* Oliver, Trans. N. Z. Inst., vol. 47, p. 512, pl. 9, figs. 1, 1a.
 1915 *Cellana hedleyi* Oliver, Trans. N. Z. Inst., vol. 47, p. 512, pl. 9, figs. 2, 2a.
 1915 *Cellana hedleyi corrugata* Oliver, Trans. N. Z. Inst., vol. 47, p. 513, pl. 9, figs. 3, 3a.
 1915 *Cellana vulcanicus* Oliver, Trans. N. Z. Inst., vol. 47, p. 513, pl. 9, figs. 4, 4a.
 1915 *Cellana scopulinus* Oliver, Trans. N. Z. Inst., vol. 47, p. 514, pl. 9, figs. 5, 5a.

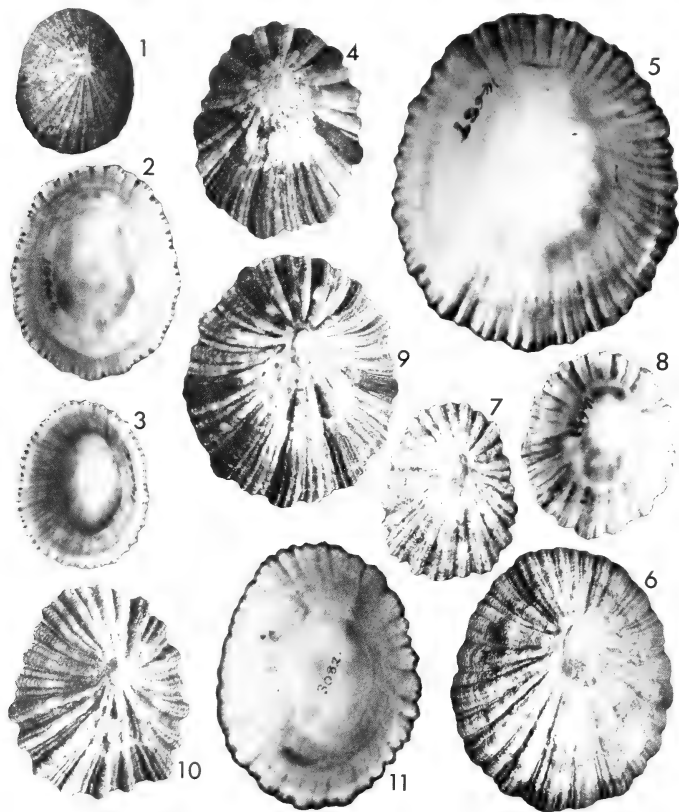


Plate 155. Figs. 1-11. *Cellana craticulata* (Suter, 1905), Kermadec Islands (continued). Figs. 1-3. Meyer Island (*vulcanica* form), 25-35 mm. (Fig. 3, compared with holotype), MF14664 & MF14665. Figs. 4-6 Raoul Island (*hedleyi* form),

32-46 mm., MF14659. Figs. 7, 8. Coral Bay, Raoul Island (*hedleyi corrugata* form), 35 mm., MF14653. Figs. 9-11. Macaulay Island (*hedleyi corrugata* form), 38-44 mm., MF3082.



Plate 156. Fig. 1. *Cellana radians* (Gmelin), New Zealand, Ti Point, Hauraki Gulf. Radula. Fig. 2. *Cellana craticulata* (Suter), Macaulay Island, Kermadecs. Radula.

Types—The holotype of *craticulatus* is in the Suter collection, New Zealand Geological Survey, Wellington, and the Oliver collection is in the Dominion Museum, Wellington.

Records—KERMADEC ISLANDS: Raoul or Sunday Island (holotype); (Auck. Mus.; AWBP coll.); Meyer Islet (AWBP coll.); Macaulay Island (Oliver, 1915); French Rock (Oliver, 1915; AWBP coll.).

Cellana denticulata (Martyn, 1784)¹

(Pl. 70, figs. 7, 8; Pl. 157, figs. 5, 6; Pl. 163, fig. 2)

Range—New Zealand: Three Kings Islands, North Island, and northern part of South Island.

Remarks—This shell is readily distinguished by its prominent brown scaly ribs, netted with brown in the interstices, and by its internal coloration, the spatula being cream to orange-brown, and the rest of the interior rayed and netted in dark-brown upon a bluish grey ground.

This is the dominant limpet of the Cook Strait area, and from there it extends southward to at least Kaikoura. In its northern range, up the North Island east coast, it reaches the Three Kings Islands, but is not generally distributed in the north. These northern isolated small colonies are situated on certain jutting points and off shore islands, which evidently are catchments for larvae transported by coastwise currents.

Description—Shell of moderate to large size, up to 74 mm. (almost 3 inches) in length, solid, elevated; regularly, closely and strongly radially

ribbed, the whole surface crossed by numerous lamellose concentric ridges that thicken into granular scales on the radials. Colour of exterior greyish, with the radials and a netted interstitial pattern in dark brown; interior brownish with the external pattern showing through strongly in brown or purplish brown. The well defined spatula varies from cream to orange-brown, and there is sometimes a bluish white area between there and the brown blotched margin.

Measurements (mm.)—

length	width	height	
74.0	63.0	37.0	Karewa Island
73.0	61.0	44.0	Karewa Island
71.5	60.0	29.0	Mt. Maunganui
52.0	43.0	19.0	Island Bay
43.5	35.0	15.0	Island Bay

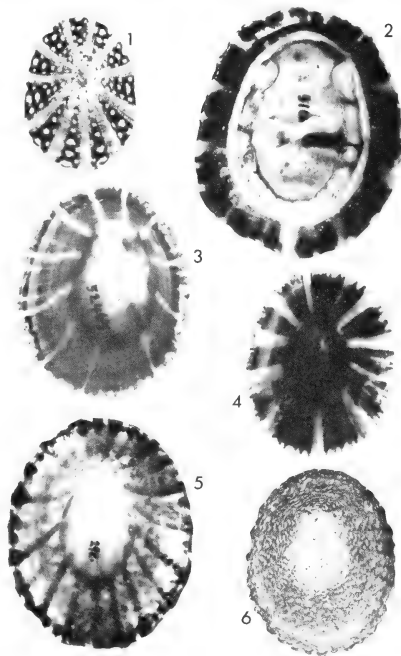


Plate 157. Figs. 1-4. *Cellana ornata* (Dillwyn, 1817), New Zealand. Fig. 1. Motutara, West Coast, Auckland, 21 mm., AWBP coll. Fig. 2. Charleston, West Coast, South Island (surf-beaten form), 42 mm., AWBP coll. 310. Fig. 3. Bluff, Southland, 42 mm., AWBP coll. 52467. Fig. 4. Campbell's Bay, Auckland, 34 mm., AWBP coll. 26270. Figs. 5, 6. *Cellana denticulata* (Martyn, 1784), New Zealand, Island Bay, Wellington, 45-48 mm., AWBP coll. 292.

¹ This name and others of Martyn, 1784, relevant to the New Zealand fauna, were validated by the International Commission of Zoological Nomenclature, in Opinion 479 (1957).

Radula—Formula $(3) + 1 + (1+0+1) + 1 + (3)$. Radula very similar to that of *radians*, with both the pair of functional centrals and the pair of laterals with long lanceolate cusps set tangentially to the shank, and the lower cutting edge of the lateral is indented in two places. The non-functional fused marginal plates have three short parallel ridges at the base as in *radians* and *flava*.

Synonymy—

- 1784 *Patella denticulata* Martyn, Univ. Conch., vol. 2, fig. 65.
Name validated by I. C. Z. N., opinion 479 (1957).
1855 *Patella imbricata* Reeve, Conch. Iconica, pl. 32, figs. 93 a, b.
1880 *Patella reevei* Hutton, Man. N. Z. Moll. p. 108, nom. nov. pro *P. imbricata* Reeve, 1855, non Turton, 1802.
1891 *Helcioniscus denticulatus*: Pilsbry, Man. Conch., vol. 13, p. 138, pl. 68, figs. 23, 24; pl. 21, figs. 49, 50.
1913 *Helcioniscus denticulatus*: Suter, Man. N. Z. Moll., p. 80, pl. 7, fig. 10.
1957 *Patella denticulata* Martyn: validation of name, I. C. Z. M. opinion 479, p. 369.

Records—NEW ZEALAND: Three Kings Islands, Great Island (AWBP); North Island; Cape Maria van Diemen (AWBP); Karewa Island, Bay of Plenty (Auck. Mus.); Mt. Maungani (AWBP coll.); Island Bay, Wellington (AWBP coll.); South Island; Goose Bay, Kaikoura (AWBP coll.).

Cellana flava (Hutton, 1873)

(Pl. 70, figs. 5, 6; Pls. 158, 159)

Range—New Zealand, east coast of both North and South Islands, from East Cape to Motanau Island, north Canterbury.

Remarks—This bright yellowish to orange limpet, long considered to be only a subspecies of *radians*, merits specific separation from that species, not only on account of its distinctive

coloration but also, by virtue of its simple yet relatively constant form of sculpture, short stubby cephalic tentacles, and peculiar vestigial central radular plate.

The species has its centre of distribution along the Kaikoura-Amuri Bluff coast of Marlborough where it occurs in great numbers on white limestone in the mid- to low-tidal zone. Like *denticulata*, its extra-limital occurrences are sporadic, and almost always on prominences of the coastline. The pale coloration possibly resulted from long association with a white limestone substratum, but if so, it cannot be a direct response, for bright-orange examples are just as likely to be found living on dark rock, notably at Whakatake, near Castle Point, in the North Island.

Description—Shell of moderate size to rather large, up to 66 mm. (over 2½ inches) in length, solid, elevated, with the apex varying from sub-central to about the anterior third. Sculpture simple and rather constant, consisting of from 19 to 25 strong, rounded, primary radials, with an occasional much weaker intermediate that develops only towards the margin. Colour, both externally and internally, pale-yellow to bright-orange. In senile examples the exterior is usually eroded to dull grey or whitish, and the interior is whitish also, except for the large spatula, which is invariably yellowish to orange. Occasional

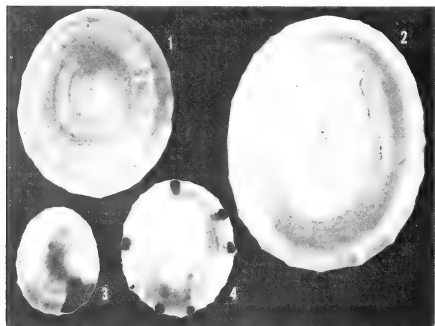


Plate 158. *Cellana flava* (Hutton, 1873). New Zealand. Fig. 1, East Cape, North Island, 41 mm., AWBP coll. 52732. Figs. 2-4, Limestone Point, Marlborough, South Island, 18-51 mm. (Note the dark rays found occasionally in some young examples; AWBP coll. 68572; Figs. 3, 4).

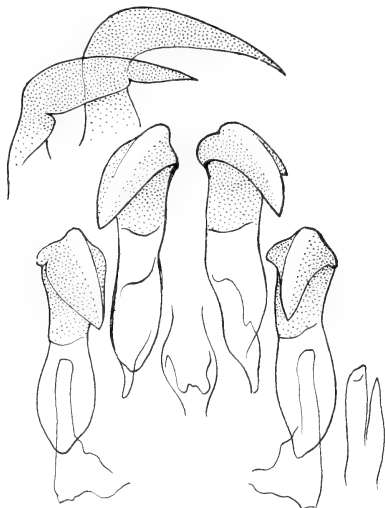


Plate 159. *Cellana flava* (Hutton), New Zealand, East Cape. Radula.

young shells have several irregularly disposed brown radial stripes developed only towards the margin.

Radula—Formula $3 + 1 + (1+(1)+) + 1 + 3$; very similar to the radula of *radians*, even to the appearance of a vertical alternation of long and short marginals, but the vestigial central plate is different, being foliated, open above, and with the front edge scalloped into five cusp-like lobes (East Cape example).

Measurements (mm.)—

length	width	height	
66.0	55.0	27.0	Karaka Point
58.0	48.5	28.0	Limestone Point
47.5	37.5	19.5	Limestone Point
35.5	29.5	14.5	Limestone Point

Synonymy—

1873 *Patella flava* Hutton, Cat. N. Z. Moll., p. 44.

1891 *Helcioniscus flavus*: Pilsbry, Man. Conch., vol. 13, p. 142.

1913 *Helcioniscus radians flavus*: Suter, Man. N. Z. Moll., p. 84; Atlas (1915), pl. 7, fig. 15.

Types—The type is in the Dominion Museum, Wellington.

Records—NEW ZEALAND: North Island; Horoera, East Cape; Gisborne; Tolaga Bay; Whakatake; Castlepoint, East Wairarapa. South Island: Karaka Bay, Queen Charlotte Sound; Limestone Point, S. of Clarence River, Marlborough (all AWBP coll.); Kaikoura, Amuri Bluff and Motanau Island (Suter, 1913).

Cellana ornata (Dillwyn, 1817)

(Pl. 70, figs. 12, 13; Pls. 157, 163)

Range—New Zealand: North, South and Stewart Islands.

Remarks—In its young non-eroded state this species has a most attractive colour pattern, the primary ribs being lilac-grey, and the intermediate areas purplish brown to black, with the nodes picked out in white. In large-sized examples the exterior is almost invariably eroded and little of the basic colour pattern remains. Also, in coastal areas subject to rigorous wave action, the profile is low, and the shape varies from elongate-ovate to broadly-ovate. This species is common on rock faces in the upper tidal zone.

Description—Shell small to moderate sized, up to 48 mm. (almost 2 inches) in length, but usually between 24 and 28 mm., solid, normally high-conical, with the apex at about the anterior third. Sculpture consisting of eleven strong, primary, radial ribs, each interspace with a central nodulose secondary radial, flanked on each side by a pair of much weaker radials; the whole crossed by dense concentric threads, that thicken like knots, wherever they surmount the primary and secondary radials. Colour of exterior: the primary ribs pale lilac-grey, the interspaces dark purplish brown to almost black,

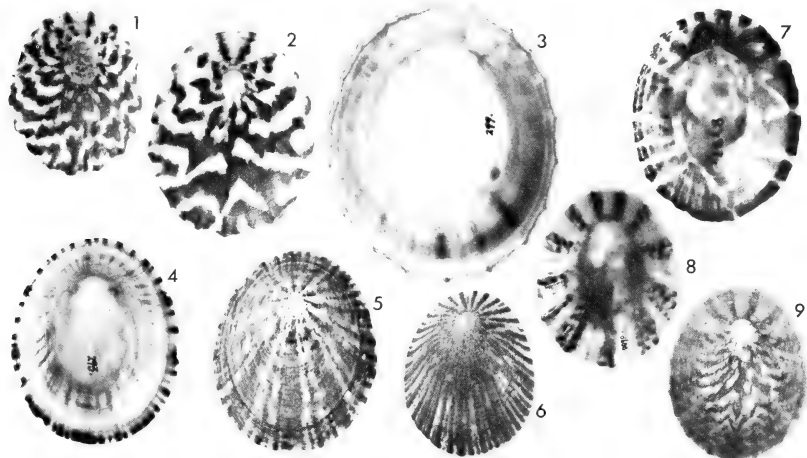


Plate 160. Figs. 1-9. *Cellana radians* (Gmelin, 1791), New Zealand. 23-65 mm. Fig. 1. *earlii* pattern, Motutara, West Coast, Auckland. AWBP coll. 252. Figs. 2-5. Mount Maungamui, Bay of Plenty, AWBP coll. 52469, 293 & 299. Figs.

6, 7. Four miles south of Clarence River, Marlborough, AWBP coll. 3783. Figs. 8, 9. Motuhihi Island, Hauraki Gulf, Auckland. AWBP coll. 18600.

with the nodes on the secondary radials picked out in white. Color of interior: with broad, dark purplish brown rays and silvery intermediate narrow rays; spatula dark chestnut-brown to almost black, often partly clouded with greyish callus.

Radula—Formula (3) + 1 + (1+0+1) + 1 + (3); similar to the radula of *radians*, the paired centrals each with a long lanceolate cusp, set tangentially to the shank, and the laterals similar but heavier, with the lower edge indented to form two denticles; the three marginals are fused into a small irregularly-shaped, semitransparent plate, without cusps.

Measurements (mm.)—(all A.W.B. Powell collection).

length	width	height	
48.0	44.5	21.0	Motutara
44.0	34.0	11.0	Charleston
42.5	35.0	21.0	Bluff
42.0	35.0	19.0	Mt. Maunganui
28.0	22.0	13.0	Motutara
22.5	18.5	7.0	Motutara

Synonymy—

- 1817 *Patella ornata* Dillwyn, Cat. Rec. Shells, vol. 2, p. 1029; based upon Martini-Chemnitz, Conch. Cab., vol. 11, p. 180, pl. 197, figs. 1914, 1915.
 1841 *Patella nodosa* Hombron & Jacquinot, Ann. Sci. Nat., vol. 2 (16), p. 191.
 1846 *Patella luctuosa* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 150.
 1855 *Patella margaritaria* Reeve, Conch. Iconica, pl. 28, figs. 74 a, b.
 1883 *Patella "denticulata"* (error for *ornata*); Hutton, Trans. N. Z. Inst., vol. 15, p. 128, pl. 16, fig. B (*radula*).
 1891 *Helcioniscus ornatus*: Pilsbry, Man. Conch., vol. 13, p. 137, pl. 68, figs. 14-19; pl. 19, figs. 39, 40.
 1913 *Helcioniscus ornatus*: Suter, Man. N. Z. Moll., p. 80; Atlas (1915), pl. 7, fig. 11.
 1913 *Helcioniscus ornatus inconspicuus*: (non Gray, 1843), Suter, Man. N. Z. Moll., p. 81; Atlas (1915), pl. 7, fig. 12.

Records—NEW ZEALAND: North Island; Cape Maria van Diemen (Auck. Mus.); Reotahi, Whangarei Heads; Motuihi Island, Auckland; Campbell's Bay, Auckland; Motutara, West Coast, Auckland; Mt. Maunganui, Bay of Plenty; Napier, North Island; 4 mi. S. of Clarence River, Marlborough; Lyttelton; Cape Foulwind; Charleston; Oamaru; Kaitiaki Beach, north Otago (all AWBP coll.); Taieri Beach, Otago (Auck. Mus.); Solander Island, Foveaux Strait (Auck. Mus.); Stewart Island; Herekopare Island (both AWBP coll.).

Cellana radians (Gmelin, 1791)

(Pl. 70, figs. 1-4; Pls. 156, 160, 161)

Range—New Zealand: North, South and Stewart Islands.

Remarks—This is the most common of the New Zealand limpets and the most variable, not only in shape and sculpture, but also in colour pattern.

The many forms of the species are outlined in the following formal description. In general, northern shells, which are the typical form, have the primary ribs coloured brown, and there is often a connecting pattern of transverse streaks (the *earlii* pattern). Most southern shells, on the other hand, have the sculpture finer, more even, the external markings indistinct, and internally there is a greenish silvery to golden lustre. This, the *perana* form, is the dominant one at Stewart Island and the southern part of the South Island, but it is known to occur also on the west coast of the North Island at Whitecliffs, north Taranaki, and also at the Three Kings Islands. On the other hand, at Cape Foulwind on west coast of the South Island both the *perana* and *earlii* forms occur together. The *earlii* pattern, which is more common in northern shells, is essentially a juvenile one, and seldom persists into the fully adult, without resolving into radial streaks, more or less confined to the primary radials.

Thomson (1919), in his paper on polymorphism in *Cellana radians* was of the opinion that colour pattern changes in the fully adult of this species were due to external erosion, accompanied by a compensating internal build-up of callus. In such senile examples only deep-seated colour, associated with the primary radials still persists.

Helcioniscus radians mestayerae Suter, 1906, is not a New Zealand shell, despite the cited locality, Stewart Island, but is based upon a wrongly labelled specimen of the Indo-Pacific *Cellana testudinaria* Linnaeus, 1758.

Description—Shell of medium to moderately large size, up to 65.5 mm. (2½ inches) in length, polymorphic, extremely variable in shape, altitude and colour pattern. Typical form ovate, depressed, with the apex at about the anterior fourth; sculptured with 20 to 25 narrow, slightly raised primary radials, and a varying number of very weak radial threads in the interspaces, but often, the latter are subobsolete; the whole surface crossed by weak, but exceedingly dense, concentric lirations. Colour of exterior greyish buff, with a reddish brown pattern of interrupted radial lines and transverse streaks; interior yellowish, with the external brown markings showing through strongly; spatula ill-defined, fawn to chestnut-brown. In the *earlii* form the transverse streaks are dominant, and join up in a concentric anastomosing pattern. In the *decora* form the pattern is restricted to radial lines; and in the *perana* form the sculpture is fine and more regular, the external coloration of dark, continuous

or intermittent, radial lines, and internally it is greenish silvery to golden, sometimes partly clouded to fully obscured by a white callus.

Radula—Formula $3 + 1 + (1+0+1) + 1 + 3$. There is a pair of strong centrals, each with a long lanceolate cusp, set tangentially to the shank, and in between these two teeth is a small, narrow, vestigial median plate; the pair of laterals are similar but have a broadly triangular base, and the lower cutting edge of the cusp is indented to form two denticles; all three marginals are present but they are very thin and semitransparent; only the inner one bears a slight cusp, and below these, joined by a thin membrane are three shorter

narrow plates, the effect being of long and short marginals in a vertical alternation.

Measurements (mm.)—(A=typical form; B=*earlii* form; C=*perana* form. All from the A. W. B. Powell coll'n.

length	width	height	
65.5	55.0	24.0	(A) Mt. Maunganui
64.5	54.5	26.0	(C) Herekopare Island
62.0	50.0	30.0	(C) Herekopare Island
59.0	50.5	16.0	(A) Mt. Maunganui
57.0	48.0	20.0	(C) Herekopare Island
46.0	37.5	12.0	(A) Motuihi Island
43.5	35.5	17.0	(C) Cape Foulwind
41.5	34.0	20.5	(C) Cape Foulwind
35.5	28.0	7.75	(B) Cape Foulwind
28.0	22.5	6.0	(A) Little Barrier Id.
18.5	15.0	3.0	(B) Little Barrier Id.

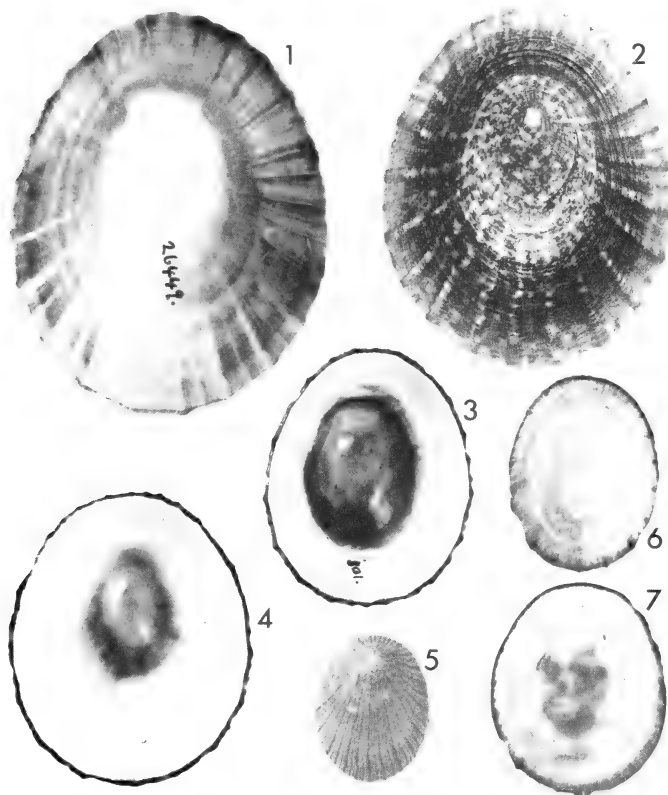


Plate 161. Figs. 1-7. *Cellana radians* (Gmelin, 1791) (*perana* form). Figs. 1, 2. Herekopare Island, Stewart Island, 57 mm., AWBP coll. 26449. Figs. 3, 4. Lyttelton, South Island, 41-44

mm., AWBP coll. 301. Figs. 5-7. North West Landing, Great Island, Three Kings Islands, New Zealand, 25-35 mm., AWBP coll. 52687.

Synonymy—

- 1791 *Patella radians* Gmelin, Syst. Nat., ed. 13, p. 3720; based upon Martini-Chemnitz, Conch. Cab., vol. 10, pl. 168, fig. 1618.
 1830 *Patella argyropsis* Lesson, Voy. Coquille, Zool., vol. 2, p. 419.
 1830 *Patella pholidota* Lesson, Voy. Coquille, Zool., vol. 2, p. 420.
 1834 *Patella argentea* Quoy and Gaimard, Voy. Astrolabe, Zool., vol. 3, p. 345, pl. 70, figs. 16, 17.
 1841 *Patella radiatilis* Hombron and Jacquinot, Ann. des Sci. Nat., vol. 16, p. 191.
 1848 *Patella orichalcea* Philippi, Zeitschr. f. Malak., p. 163.
 1849 *Patella decora* Philippi, Zeitschr. f. Malak., p. 162.
 1854 *Patella decora* Philippi, Reeve, Conch. Iconica, pl. 15, figs. 33 a-c.
 1855 *Patella earlii* Reeve, Conch. Iconica, pl. 27, figs. 71 a, b.
 1873 *Patella flexuosa* (non Quoy and Gaimard, 1834), Hutton, Cat. Mar. Moll. N. Z., p. 45.
 1874 *Patella antipodum* E. A. Smith, Voy. Erub. & Terr. Moll., p. 4, pl. 1, fig. 25.
 1882 *Patella olivacea* Hutton, N. Z. Journ. Sci., vol. 1, p. 69.
 1891 *Helcioniscus radians* Gmelin, Pilsbry, Man. Conch., vol. 13, p. 139, pl. 23, figs. 4, 6, 7, 8; pl. 69, figs. 25-31, 34-37 (non figs. 32, 33, 38 & 39).
 1913 *Helcioniscus radians* Gmelin, Suter, Man. N. Z. Moll., p. 81, pl. 7, fig. 13.
 1913 *Helcioniscus radians argenteus* Q. and G., Suter, Man. N. Z. Moll., p. 82.
 1913 *Helcioniscus radians decorus* Philippi, Suter, Man. N. Z. Moll., p. 82.
 1913 *Helcioniscus radians earlii* Reeve, Suter, Man. N. Z. Moll., p. 83.
 1913 *Helcioniscus radians olivaceus* Hutton, Suter, Man. N. Z. Moll., p. 84.
 1915 *Cellana radians perana* Iredale, Trans. N. Z. Inst., vol. 47, p. 432; non nov. pro *Patella olivacea* Hutton, 1882; non Anton, 1839.

- 1919 *Cellana radians* Gmelin, Thomson, N. Z. Journ. Sci. Tech., vol. 2, pp. 264-267 (polymorphism).
 1923 *Helcioniscus radians* Gmelin, Eales, Brit. Antarct. ('Terra Nova') Exped., 1910, Moll., pt. 5, pp. 3-6, text, fig. 2 (radula).

Records—NEW ZEALAND (typical form): Three Kings Islands. Great Island (F. Climo, 1970); North Island: Cape Maria van Diemen (Auck. Mus.); Busby Head, Whangarei Heads; Little Barrier Island; Motuhi Island, Auckland; Motutara, west coast, Auckland; Mt. Maunganui, Gisborne; Tolaga Bay; Island Bay, Wellington. South Island: Cape Foulwind (all AWBP coll.); Lyttelton (AM.); Dowling Bay, Dunedin (Auck. Mus.); Stewart Island; The Neck, Patterson Inlet (AWBP coll.).
(perana form): North Island: White Cliffs, north Taranaki. South Island: Goose Bay, Kaikoura; Cape Foulwind; Waimui, Akaroa; Lyttelton; Charleston; Purakanui, Otago; Timaru, Otago; St. Clair, Dunedin; Ocean Beach, Bluff. Stewart Island; Herekopare Island (all AWBP coll.).

Cellana stellifera (Gmelin, 1791)

(Pl. 70, figs. 9-11; Pls. 162, 163)

Range—New Zealand; North, South and Stewart Islands.

Remarks—This species lives at and just below low tide on smooth rock faces in clean water situations but is not generally common. It is easily recognised by its reddish brown external colour, bluish silvery interior, and usual presence of an apical star in paler colour. It is more abundant in the northern part of its range.

Description—Shell of moderate size, 30 to 71 mm. (1½ to 2¾ inches) in length, broadly ovate and of low to moderate height, with the apex at about the anterior third, sculptured with numerous low rounded radial ridges, crossed by dense delicate concentric growth lamellae; margin weakly scalloped. Colour, externally dark reddish brown, mostly showing a white or pale yellowish star at the apex, this often persisting to the adult stage, and occasionally with long rays extending from the points of the star right to the margin; interior bluish or purplish grey with a silvery sheen, the star pattern usually showing through; spatula ill-defined, a chestnut smear often clouded by a whitish callus.

Measurements (mm.)—

length	width	height	
71.0	58.0	19.0	Whangarei Heads
57.5	47.5	19.0	Whangarei Heads
45.5	37.0	14.0	Whangarei Heads
33.0	26.5	10.5	Rocks Road, Nelson

Synonymy—

- 1791 *Patella stellifera* Gmelin, Syst. Nat. ed. 13, p. 3719, based upon Martini-Chemnitz, Conch. Cab., vol. 10, pl. 168, fig. 1617.

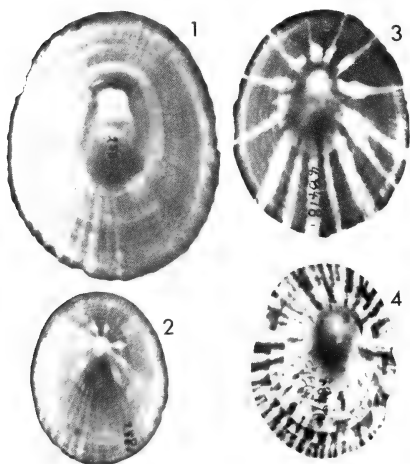


Plate 162. *Cellana stellifera* (Gmelin, 1791), New Zealand. Figs. 1, 2. Island Bay, Wellington, 33-50 mm., AWBP coll. 258. Figs. 3, 4. Rocks Road, Nelson, 29-33 mm., AWBP coll. 48478.

- 1834 *Patella stellularia* Quoy and Gaimard, Voy. Astrolabe, Zool., vol. 3, p. 347, pl. 70, figs. 18-20.
 1855 *Patella stellularia* Q. and G. Reeve, Conch. Iconica, pl. 33, figs. 96 a, b.
 1891 *Helcioniscus stellifera* Q. and G., Pilsbry, Man. Conch., vol. 13, p. 141, pl. 70, figs. 43-45.
 1905 *Helcioniscus stelliferus phymatius* Suter, Proc. Malac. Soc., Lond., vol. 6, p. 350, text fig.
 1913 *Helcioniscus stelliferus* Q. and G., Suter, Man. N. Z. Moll., p. 86; Atlas (1915), pl. 7, fig. 21.
 1915 *Cellana stellifera*: Iredale, Trans. N. Z. Inst., vol. 47, p. 432.

Types—The Martini-Chemnitz specimens are possibly in the University Museum, Copenhagen. The cited type locality "Friendly Islands" is erroneous.

Records—NEW ZEALAND: North Island: Cape Maria van Diemen (Auck. Mus.); Busby Head, Whangarei Heads; Little Barrier Island; Kawau Island; Mt. Maunganui; Island Bay, Wellington. South Island: Rocks Road, Nelson (all AWBP coll.); New Brighton (Suter, 1913). Stewart Island: Euchre Creek (AWBP coll.). (Suter's Campbell Island record is based erroneously upon *Patinigera terroris* (Filhol, 1850)).

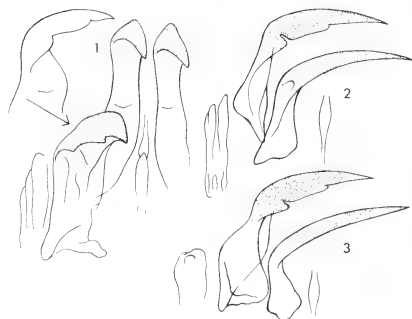


Plate 163. Radulae of New Zealand *Cellana*. Fig. 1. *Cellana stellifera* (Gmelin), Ti Point, Hauraki Gulf, Auckland. Fig. 2. *Cellana denticulata* (Martyn), Makara, Wellington. Fig. 3. *Cellana ornata* (Dillwyn), East Cape, North Island. In figs. 2 and 3 the centrals and laterals are shown in semi-profile.

Key to the subspecies of *Cellana strigilis*

1. Nucleus at anterior third to seventh of shell
 - A. Shell held to light showing pale spots and shapes (ocellate)
 - a. Outline broadly ovate

External colour bluish white, rayed and blotched with light-brown;
 internal pattern dark-rayed, interrupted at margin *redimiculum*

External colour almost completely clouded sooty-grey to dark-brown;
 internal pattern dark-rayed, confluent at margin *strigilis*
 - b. Outline narrowly ovate

External colour almost completely clouded with olive-brown;
 internal pattern dark-rayed, connected at margin *flemingi*
 - B. Shell held to light showing dense pattern of irregular narrow radials

External colour greenish grey, with dense pattern of brown radials;
 internal pattern dark-rayed, interrupted at margin *bollonsi*

Outline broadly ovate *chathamensis*
2. Nucleus at anterior 10th to 27th of shell; shell held to light showing heavy radial streaks; outline narrowly ovate; external colour bluish white, rayed and heavily blotched; internal pattern dark-rayed, interrupted at margin *oliveri*

Cellana strigilis (Hombron and Jacquinot, 1841)

Range—South Island, Stewart Island, Chatham Islands, and southern islands of New Zealand.

Remarks—The genus *Cellana* is typically warm-water Indo-Pacific distribution, so it is remarkable to find the genus extending to as far south as Campbell Island, 52° 30'S. These occurrences are probably relict from former warmer geologi-

cal times, for all the islands concerned stand upon the extensive submarine platform surrounding New Zealand (See Plate 99).

Subspecies have developed in isolation, and although they are all closely allied, recognisable differences are apparent in the shells from these segregated populations. A key to these subspecies follows:

Cellana strigilis subspecies
strigilis (Hombron and Jacquinot, 1841)

(Pl. 70, figs. 14, 15; Pls. 164, 168)

Range—Auckland and Campbell Islands, southern New Zealand.

Remarks—The southern islands' *strigilis* and the mainland *redimiculum* are closely allied, but always easily distinguished by the fact that the former is dark, with the interior sooty-grey, having an underlying densely mottled pattern in dark-brown, which forms an approximately continuous dark margin to the shell. On the other hand, *redimiculum* is yellowish brown, with dark

reddish brown radials that do not anastomose at the margin.

Description—Shell large, up to 80 mm. (3¼ inches) in length, solid, broadly-ovate, elevated, with the apex varying between the anterior third and sixth. Sculpture consisting of 20 to 25 strong, rounded, radial ribs, mostly with a weaker radial in each interspace; the whole surface crossed by dense, weak, concentric growth lines. Colour of exterior dark brown or greenish, to almost black, with a few spots and streaks of yellowish-white, much more prominent when the shell is held to the light; interior purplish-brown to sooty-grey, clouded and indistinctly rayed with dark brown;

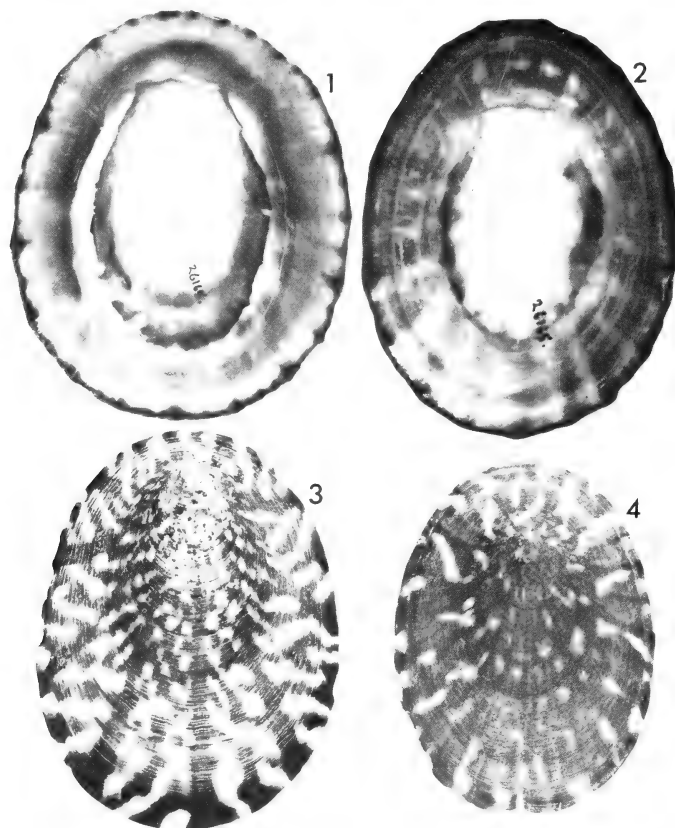


Plate 164. *Cellana strigilis* (Hombron & Jacquinot, 1841). Figs. 1, 2, Perseverance Harbour, Campbell Island, 78 mm., AWBP coll. 26165. Fig. 3, Under South Col, Campbell Is-

land, 37 mm., AWBP coll. 42168. Fig. 4, Garden Cove, Campbell Island, 46 mm., AWBP coll. 42169.

spatula light yellowish-brown, irregularly margined in dark grey. In non eroded young shells the ground colour varies from russet-brown through greenish grey to almost black, with the interstitial odd spots and splashes pale bluish.

Measurements (mm.).—

length	width	height	
80.0	68.0	39.0	Campbell Island
77.5	66.5	30.0	Campbell Island
70.0	60.0	34.0	Shoal Pt., Campbell Id.
65.0	52.0	46.0	Shoal Pt., Campbell Id.
57.0	42.5	17.0	Garden Cove, Campbell Id.
38.0	31.0	12.5	Garden Cove, Campbell Id.

Synonymy—

- 1841 *Patella strigilis* Hombron and Jacquinot, Ann. Sci. Nat., vol. 2, pt. 16, p. 190.
 1846 *Patella illuminata* Gould, Proc. Boston Soc. Nat. Hist., vol. 2, p. 149.
 1891 *Helcioniscus strigilis* H. and J., Pilsbry, Man. Conch., vol. 13, p. 137.
 1891 *Helcioniscus illuminata* Gould, Pilsbry, Man. Conch., vol. 13, p. 142, pl. 70, figs. 40-42.
 1913 *Helcioniscus strigilis* (in part): Suter, Man. N. Z. Moll., p. 87.
 1924 *Cellana radians* Gmelin, Odhner, N. Z. Moll., Pap. Mortensen Pacific Exped., p. 11 (non Gmelin, 1791).
 1927 *Nacella strigilis* H. and J. Finlay, Trans. N. Z. Inst., vol. 57, p. 387.
 1955 *Cellana strigilis strigilis* H. and J. Powell, D. S. I. R., Cape Exped. Ser., Bull. no. 15, p. 70.

Types—The type of *strigilis* is in the Muséum National d' Histoire Naturelle, Paris, and that of *illuminata* in the United States National Museum, Washington.

Records—Southern islands of New Zealand: AUCKLAND ISLANDS (type): Musgrave Peninsula; Tagua Bay, Carnley Harbour; Crozier Point; Waterfall Inlet; Rose Island, Port Ross, and Enderby Island (NZGS); Carnley Harbour; Hanfield Inlet (both AWBP coll.). CAMPBELL ISLAND: Perseverance Harbour (NZGS; AWBP coll.); Shoal Point (Auck. Mus.); Monument Harbour (Cape Exped., 1945).

Cellana strigilis subspecies *bollonsi* Powell, 1955

(Pl. 165, figs. 1, 2)

Range—Antipodes Islands, southern New Zealand.

Remarks—This subspecies is easily recognised by its dense pattern of interstitial brown lines and streaks on a greenish grey ground. Occasionally the subspecies *chathamensis* has a similar pattern in juvenile shells, but it never persists into the adult stage, as it does invariably in *bollonsi*.

Description—Shell of moderate size to relatively large, up to 70.5 mm. (2¾ inches) in length, solid, narrowly ovate, depressed to moderately eleva-

ted, with the apex varying between the anterior fifth and seventh. Sculpture developing from scarcely raised radial folds in juveniles to from 20 to 24 narrowly rounded, sharply raised ribs in the adult. Colour of exterior greenish-grey, the radials marked out in light-brown to reddish-brown, plus a dense overall pattern, in these same colours, in the form of interstitial meandering radial lines and streaks; interior metallic dull blue-grey, with reddish-brown external pattern showing through; spatula buff to pale brown.

Measurements (mm.).—

length	width	height	
70.5	58.0	28.0	Antipodes Ids.
62.0	49.0	21.0	Antipodes Ids.
48.5	36.0	15.0	Antipodes Ids.
48.0	34.8	14.5	Antipodes Ids.
42.0	32.0	12.0	Antipodes Ids.

Synonymy—

- 1955 *Cellana strigilis bollonsi* Powell, Dept. Sci. and Indust. Res., Cape Exped. Ser., Bull. no. 15, p. 73, pl. 5, figs. 51-53.

Types—The holotype and paratypes are in the Dominion Museum, Wellington.

Records—ANTIPODES ISLANDS (holotype and paratypes); (AWBP coll.).

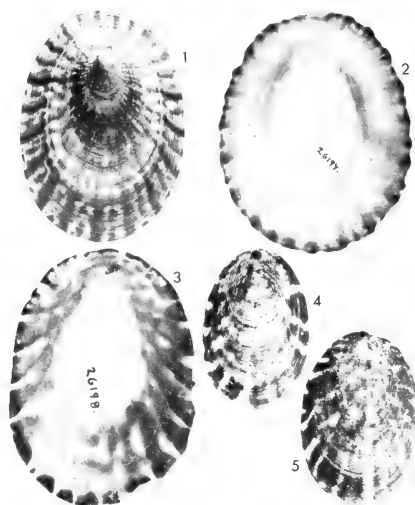


Plate 165. Figs. 1, 2. *Cellana strigilis* subspecies *bollonsi* Powell, 1955, Antipodes Islands, 48-62 mm., AWBP coll. 26197, 28420. Figs. 3-5 *Cellana strigilis* subspecies *oliveri* Powell, 1955, Bounty Islands, 35-47 mm., AWBP coll. 26198.

Cellana strigilis* subspecies *chathamensis
(Pilsbry, 1891)

(Pl. 167; Pl. 168, fig. 1)

Range—Chatham Islands, New Zealand.

Remarks—This subspecies resembles *redimiculum* in its simple radiate reddish brown radials, not coalescent at the margin, but the shape is more roundly arched, and the ocellate pattern is not in evidence. On the other hand some juveniles have a dense meandering pattern, reminiscent of the *ballonsi* pattern.

Description—Shell of moderate to large size, up to 73.5 mm. (2½ inches), in length, solid, ovate, elevated, and roundly arched in profile, with the apex at about the anterior third. Sculpture consisting of from 21 to 25 moderately strong,

rounded, radial ribs, with a weaker one in most interspaces; the whole surface crowded with concentric growth lines, weak over the early stages of the shell but stronger towards the margin, where they become slightly knotted across the radials. Colour of exterior pale yellowish-brown to greyish lilac, the radials lined in reddish brown; internally, silvery to yellowish brown, with regular reddish brown radial lines, corresponding to the external ribbing, their terminal points not coalescent at the margin; spatula large, fawn to orange-brown. Juvenile shells pale yellowish to almost black, with the pattern varying from a few radial lines to a dense coverage of meandering lines and streaks.

Measurements (mm.)—

length	width	height	
73.5	56.5	35.0	Chatham Island
70.0	55.0	31.0	Chatham Island
62.0	49.0	23.5	Chatham Island
57.5	47.5	27.0	Waitangi, Chathams
56.5	45.5	20.0	Waitangi, Chathams
39.5	30.0	11.0	Pitt Id., Chathams

Synonymy—

- 1891 *Acmaea chathamensis* Pilsbry, Man. Conch., vol. 13, p. 56, pl. 35, figs. 43-46.
 1933 *Cellana chathamensis*: Powell, Rec. Auck. Inst. Mus., vol. 1 (4), p. 196, pl. 36, figs. 1-4.
 1955 *Cellana strigilis chathamensis*: Powell Dept. Sci. and Indust. Res., Cape Exped. Ser., Bull. no. 15, p. 73.

Types—The type material is in the Academy of Natural Sciences of Philadelphia.

Records—NEW ZEALAND: CHATHAM ISLANDS (type): Waitangi (AWBP coll.); Wharekauri (AWBP coll.); Tioriori (Auck. Mus.); Waihere Bay, Pitt Island (Auck Mus.).

Cellana strigilis
subspecies ***flemingi*** Powell, 1955

(Pl. 168, fig. 3; pl. 169, figs. 5-7)

Range—Snares Islands, southern New Zealand.

Remarks—This subspecies is more closely allied to typical *strigilis* than it is to *redimiculum*, from both of which it differs in its consistently more narrowly oval shape, high arched profile, and anterior position of the nucleus.

Description—Shell of small to medium size, up to 53 mm. (2½ inches) in length, narrowly ovate, with the apex varying between the anterior fourth to fifth in adults, but one eighth or less in juveniles. Anterior slope straight, but posterior slope prominently arched, and flattened on top

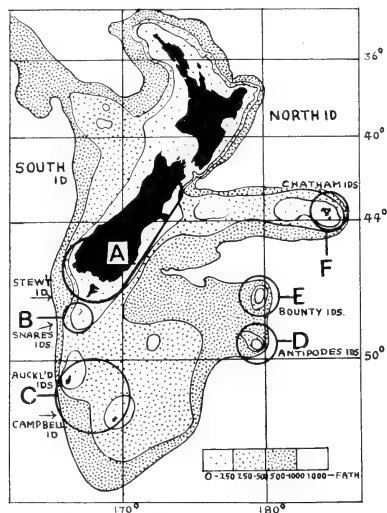


Plate 166. Distribution of *Cellana strigilis* and its subspecies. An example of an otherwise warm-water genus, surviving cooling temperatures in southern New Zealand, and represented as relict subspecies in the isolated southern islands, once part of a greater New Zealand land mass.

- A- *Cellana strigilis redimiculum* (Reeve), South Island and Stewart Island. Note northern limit near top of South Island east coast.
 B- *Cellana strigilis flemingi* Powell, Snares Islands.
 C- *Cellana strigilis strigilis* (Hombrow & Jacquimot), Auckland Islands and Campbell Island.
 D- *Cellana strigilis ballonsi* Powell, Antipodes Islands.
 E- *Cellana strigilis oliveri* Powell, Bounty Islands.
 F- *Cellana strigilis chathamensis* (Pilsbry), Chatham Islands.
 (Chart adapted from Fleming, 1951, N. Z. Science Review, 9 (10), p. 167).

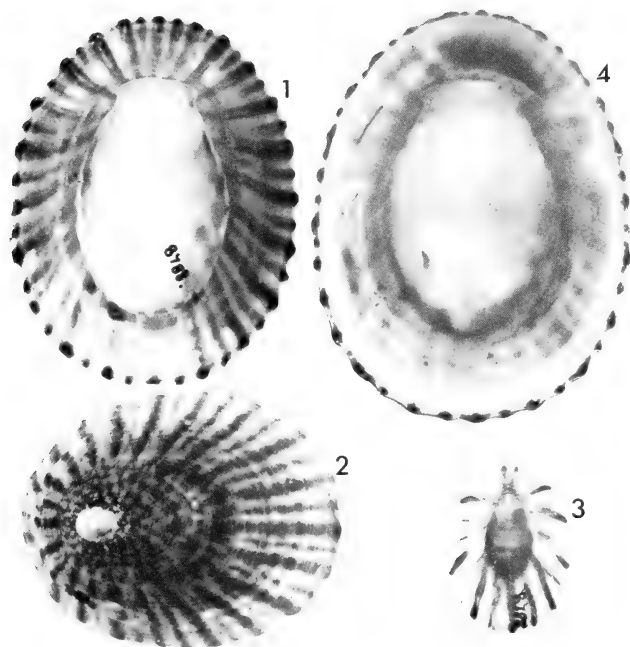


Plate 167. Figs. 1-4. *Cellana strigilis* subspecies *chathamensis* (Pilsbry, 1891). Waitangi, Chatham Islands. 21-71 mm., AWBP coll. 8786, 8788.

for about one third of the length. Sculpture consisting of about 25 narrowly rounded primary radials, and a few very weak intermediates. Young shells have the radials as scarcely raised folds, crossed by dense concentric growth lines. Colour of exterior almost uniformly olive-brown, except for the nuclear area to about 15 mm., which is dark-brown, with a light bluish ocellate pattern in the rib interstices; interior metallic dull smoky-grey, with a dark brown internal rib pattern showing through the glaze, and coalescing at the margin, in adults, to form an almost continuous border; spatula buff, tinged posteriorly with pale reddish brown.

Measurements (mm.)—

length	width	height	
53.00	41.5	22.00	holotype
47.00	35.5	18.50	paratype
28.75	21.0	7.00	paratype
21.25	15.0	4.25	paratype
17.75	12.5	3.40	paratype

Synonymy—

1955 *Cellana strigilis flemingi* Powell, Cape Exped. Ser., Bull. no. 15, p. 72, pl. 5, figs. 45-47

Types—The holotype and paratypes are in the New Zealand Geological Survey, Wellington.

Records—SNARES ISLANDS: boat harbour, on intertidal rocks.

Cellana strigilis
subspecies *oliveri* Powell, 1955

(Pl. 165, figs. 3-5)

Range—Bounty Islands, southern New Zealand.

Remarks—This subspecies is easily recognised by its narrowly ovate and depressed shape, with the apex at, or near to, the anterior end, and a bold pattern of radial streaks and blotches.

Description—Shell of small to medium size, up to 57.5 mm. (2¼ inches) in length, solid, rather narrowly ovate and depressed, the apex near to the anterior margin at all stages of growth. From

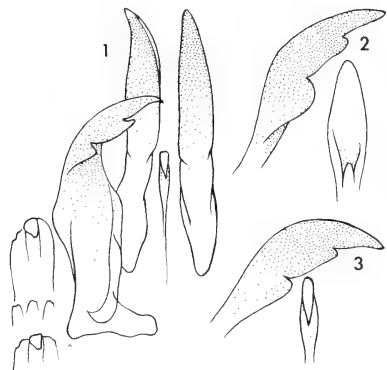


Plate 168. Radulae of New Zealand *Cellana*. Fig. 1. *Cellana strigilis* (Hombron & Jacquinot), Campbell Island. Fig. 2. *Cellana strigilis chathamensis* (Pilsbry), Wharekauri, Chatham Island. Fig. 3. *Cellana strigilis flemingi* Powell, Snares Islands. In figs. 2 and 3 the lateral, in semi-profile, and the median vestigial central only, are shown.

20 to 25 broadly rounded radial ribs, with an occasional weak interstitial one; surface smooth, apart from weak growth lines. Colour of exterior bluish-white, heavily blotched and streaked with light to dark-brown, the pattern frequently running together, leaving elongated patches of the pale ground colour; interior pale amber, with the external pattern showing through in dark brown; spatula dark-brown in young shells, to clouded with buff or pale-brown in adults.

Measurements (mm.)—

length	width	height	
57.5	45.00	20.00	paratype
41.0	29.00	10.50	holotype
35.0	24.00	7.00	AWBP coll.
27.3	20.10	6.00	paratype
16.5	10.5	4.00	AWBP coll.

Synonymy—

1955 *Cellana strigilis oliveri* Powell, Dept. Sci. and Indust. Res., Cape Exped. Ser., Bull. no. 15, p. 73, pl. 5, figs. 48-50.

Types—The holotype and paratypes are in the Dominion Museum, Wellington.

Records—BOUNTY ISLANDS (Domin. Mus., Wellington); (AWBP coll.)

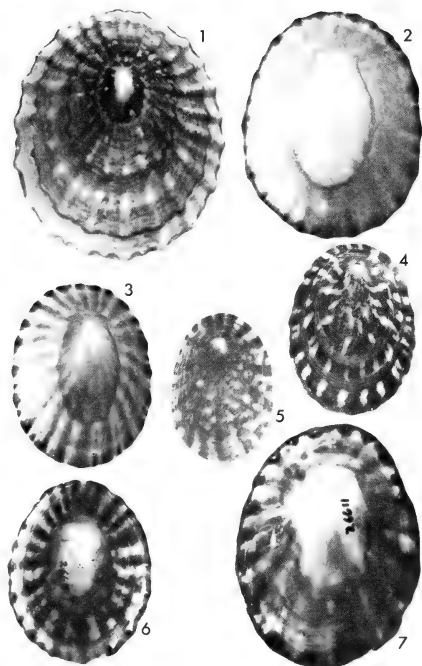


Plate 169. Figs. 1-4. *Cellana strigilis* subspecies *redimiculum* (Reeve, 1854), New Zealand. Fig. 1. Stewart Island, 78 mm., AWBP coll. 40089. Figs. 2-4. Kartigi Beach, North Otago, 30-62 mm., AWBP coll. 6874. Figs. 5-7. *Cellana strigilis* subspecies *flemingi* Powell, 1955, Snares Islands, southern islands of New Zealand, 30-50 mm., AWBP coll. 26611.

***Cellana strigilis*
subspecies *redimiculum* (Reeve, 1854)**

(Pl. 70, figs. 17-19; Pl. 169, figs. 1-4)

Range—NEW ZEALAND: Stewart Island, eastern and western Otago, and east coast of South Island as far north as Kaikoura.

Remarks—This is the common South Island mainland subspecies of *strigilis*, easily recognised by its orange-brown exterior, with pale blue ocellate flecks in the rib interstices, and internally, by the dark brown radials, that do not anastomose at the margin. The centre of distribution is eastern Otago, where it is a common intertidal limpet.

Description—Shell rather large, up to 77 mm. (3 inches) in length, solid, broadly ovate, elevated, with the apex at about the anterior fourth or fifth. Sculpture consisting of about 20 strong rounded radial ribs, mostly with a much weaker radial in each interspace; the whole surface crossed by dense weak concentric growth lines. Colour of exterior orange-brown, with pale blue ocellate flecks and streaks in the radial interspaces; interior yellowish to greyish-brown, with a golden sheen, and the external rayed pattern showing through; spatula chestnut coloured, often clouded with a greyish callus. The margin bears a regular series of dark brown spots, marking the terminal points of the external primary radials.

Measurements (mm.)— (all A.W.B. Powell collection).

length	width	height	
77.0	65.0	33.0	Stewart Island
66.5	55.0	30.0	Kartigi
51.5	43.0	21.0	Kartigi
48.0	36.0	14.0	Kartigi
30.0	22.0	10.0	Kartigi
35.5	27.5	10.5	Goose Bay

Synonymy—

- 1854 *Patella radians* Gmelin, Reeve, Conch. Iconica, pl. 12, figs. 25a, b. (non Gmelin, 1791).
 1854 *Patella redimiculum* Reeve, Conch. Iconica, pl. 20, figs. 50a, b.
 1873 *Patella pottsi* Hutton, Cat. Mar. Moll. N.Z., pp. 44.
 1891 *Helcioniscus redimiculum* Reeve, Pilsbry, Man. Conch., vol. 13, p. 136, pl. 23, figs. 1, 2, 3, 5.
 1913 *Helcioniscus strigilis* (in part, non Hombron and Jacquinot, 1841): Suter, Man. N. Z. Moll., p. 87.
 1913 *Helcioniscus redimiculum* (in part): Suter, Man. N. Z. Moll., p. 85.
 1927 *Nacella redimiculum* Reeve, Finlay, Trans. N. Z. Inst., vol. 57, pp. 337, 338.
 1955 *Cellana strigilis redimiculum* Reeve, Powell Dept. Sci. and Indust. Res., Cape Exped. Ser., Bull. no. 15, p. 71.

Types—The type of *redimiculum* is in the British Museum (Natural History).

Records—NEW ZEALAND: South Island: Goose Bay, Kaikoura; Oamaru; Kartigi Beach, Otago; Waikouaiti, Otago; Portobello, Dunedin; St. Clair, Dunedin (all AWBP coll. 280); entrance to Milford Sound (Galathea Exped., Sta. 624); Henrietta Bay, Ruapuke Island, Foveaux Strait (Auck Inst.); Stewart Island (AWBP coll.); Blind Passage, Port Pegasus (Auck. Inst.).

Cellana thomsoni Powell and Bartrum, 1929

(Pl. 171, fig. 1)

Range—New Zealand, lower Miocene.

Remarks—The species is unlike any other New Zealand member of the genus, but bears some resemblance to the Japanese Recent *toreuma* Reeve. In the Japanese species, however, the radials are not so strongly or so numerous beaded.

Description—Shell small, 14 mm. (9/16 of an inch) in length, but probably attained a much larger size, elongate-ovate, depressed, with the apex at about the anterior sixth. Sculpture consisting of about 36 primary narrowly rounded radials, and 1 to 3 secondary radials in the interspaces. The whole surface is crossed by very numerous concentric lamellose growth lines, that thicken to become knotted or beaded where they cross the radials.

Measurements (mm.)—

length	width	height	
14.0	10.0	21.1	holotype

Synonymy—

- 1929 *Cellana thomsoni* Powell and Bartrum, Trans. N. Z. Inst., vol. 59, p. 413, pl. 35, fig. 12.

Types—The holotype, the only known specimen, is in the Geology Department, University of Auckland.

Records—NEW ZEALAND: Waiheke Island, Oneroa Beds, Waitemata Group, Otian Stage, lower Miocene.

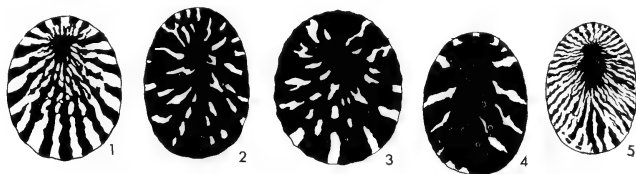


Plate 170. Juvenile colour patterns, by transmitted light, in New Zealand *Cellana strigilis* and subspecies. Fig. 1. *C. strigilis redimiculum* (Reeve), Oamaru, South Island. Fig. 2. *C. strigilis flemingi* Powell, Snares Islands. Fig. 3. *C. strigilis*

strigilis (Hombron & Jacquinot), Auckland Islands. Fig. 4. *C. strigilis oliveri* Powell, Bounty Islands. Fig. 5. *C. strigilis bollonsi* Powell, Antipodes Islands. The line is drawn through the apices.

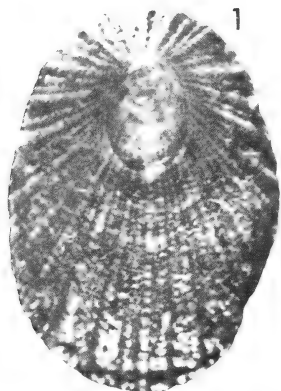


Plate 171. Fig. 1. *Cellana thomsoni* Powell & Bartrum, 1929. New Zealand, Waiheke Island, Auckland, Otaian, lower Miocene, 14 mm., holotype.

***Cellana cophina* Powell, new species**

(Pl. 172, fig. 1)

Range—New Zealand. Cape Rodney, Hauraki Gulf (holotype), and coast $\frac{1}{2}$ mile east of Goat Island, Cape Rodney (paratype). Motutapu Island, Auckland; all in either coarse sandstone or conglomerate, basal Waitemata Beds, Otaian, lower Miocene.

Remarks—This strongly sculptured species is nearest allied to the Recent *denticulata* (Martyn, 1784), from which it differs in that both the radial ribs and the concentric cords are so strong that a coarse basket-weave effect results.

Description—Shell rather large, 60 to 70 mm. ($2\frac{1}{2}$ — $2\frac{3}{4}$ inches) in length, narrowly ovate and of low profile, with the apex at about the anterior third. Sculpture very strong, like a coarse basket-weave, consisting of about 20 strong rounded radials, without intermediates, and crossed by closely spaced prominent cords that are much thickened where they cross the radials, but weak in the interspaces.

Measurements (mm.)—Estimated size in parentheses.

length	width	height
55.0 (57.0)	43.5 (47.0)	(15.0) holotype
65.0 (70.0)	16.0	(16.0) paratype

Types—Holotype and paratype in the collection of the New Zealand Geological Survey, Wellington. The type locality is Cape Rodney, Hauraki Gulf, New Zealand.

***Cellana taberna* Powell, new species**

(Pl. 172, fig. 2)

Range—New Zealand. Curiosity Shop, Rakaia, South Island, Waitakian greensands, lower Miocene.

Remarks—This shell has distinctive sculpture, unlike that of any of the described species from New Zealand or elsewhere. The sculpture differs from that of *C. cophina* in that is a combination of large irregularly-oval, smooth blisters on the primary radials with much weaker and more regular interstitial riblets that are cut into small, squarish nodes by deeply-incised concentric grooves.

Description—Shell small, probably not adult, 23 mm. ($\frac{1}{2}$ of an inch) in length, narrowly ovate, and of low profile, with the apex at the anterior third. Sculpture very strong, consisting of about 13 prominent rounded primary radials that develop large ovate smooth blisters, stronger posterior to the apex. Interspaces with from 2 to 5 secondary radials, crossed by deeply incised concentric grooves, cutting them into series of small rectangular nodes.

Measurements (mm.)—

length	width	height
22.5	17.25	6.25 holotype

Type—The unique holotype is in the collection of the New Zealand Geological Survey, Wellington. The type locality is stated in the range above.

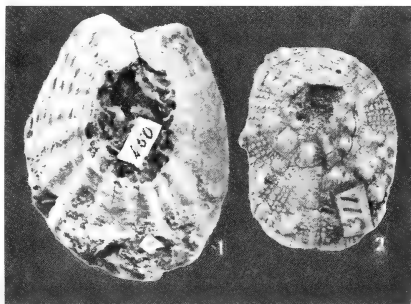


Plate 172. Fig. 1. *Cellana cophina* new species. New Zealand, Cape Rodney, Hauraki Gulf, North Island, Otaian, lower Miocene; holotype, 55 (57) mm. Fig. 2. *Cellana taberna* new species. New Zealand, Curiosity Shop, Rakaia, South Island, Waitakian greensands, lower Miocene; holotype, 22.5 mm.

Genus *Nacella* Schumacher, 1817Type *Patella mytilina* Helbling, 1779

This genus and its subgenus *Patinigera* are characteristic molluscs of Antarctic and Subantarctic seas. They have their centre of distribution in the Magellanic Province of southern South America from whence the seaweed-dwelling species in particular tend to spread eastward, being assisted to a considerable extent by the prevailing West Wind Drift that operates strongly in the Subantarctic Zone.

Although *Nacella* and *Patinigera* are not members of the Indo-Pacific fauna, the recognised species are listed and briefly described here, since many of them do occur in waters to the south of both the Indian and Pacific Oceans, and at one location, Campbell Island, in the New Zealand faunal area, both *Nacella* (*Patinigera*) and the warmer-water derived *Cellana* flourish side by side.

Both *Nacella* and *Patinigera* differ from all other Patellidae in the presence of an epipodial fringe, a scalloped lamellate flange that occupies a mid position between the edge of the foot and the gill cordon, except where it is interrupted by the head region.

There is a link with *Patella* in that the gill cordon is complete, not interrupted by the head as it is in *Cellana*. The dentition, on the other hand, with its pair of centrals, alternating with a pair of laterals, is comparable with that of *Cellana*, not short, straight and bent back upon itself at the nascent end as it is in *Patella*.

Thiele in 1929 proposed the subfamily Nacellinae for *Nacella*, *Patinigera* and *Cellana*, but the epipodial fringe, characteristic of *Nacella* and its subgenus *Patinigera*, is not found in *Cellana* or in any other patellid genus.

The radula, on the other hand, is very similar in all three of the above mentioned taxa, but very different from that of the Patellinae.

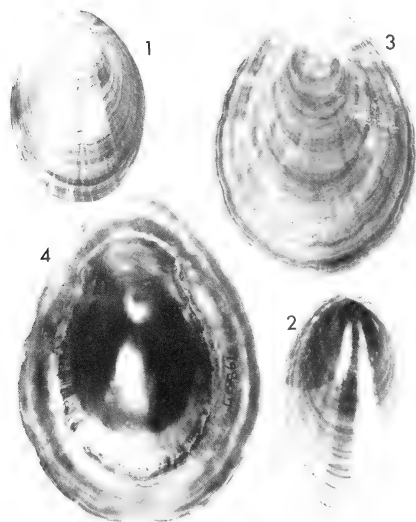


Plate 173. Figs. 1, 2. *Nacella mytilina* (Helbling, 1779). Mouth of Santa Cruz River, Patagonia, 27-29 mm., AWBP coll. 42389. Figs. 3, 4. *Nacella kerguelensis* (E. A. Smith, 1877). Fig. 3. Swain's Bay, Kerguelen Island, 43 mm., AWBP coll. 30635. Fig. 4. Heard Island, 64 mm., AWBP coll. 40861.



Plate 174. Fig. 1. *Nacella mytilina* (Helbling). Kerguelen Island. Radula, from Thiele, in Tröschel & Thiele, 1891, pl. 28, fig. 30. Fig. 2. *Nacella (Patinigera) deaurata* (Cmelin). Tuesday Bay. Radula, from Thiele, in Tröschel & Thiele, 1891, pl. 28, fig. 32. Fig. 3. *Nacella (Patinigera) terroris* (Filloh). Campbell Island. Radula.

Description—Shell rather small to moderately large, thin and fragile, typically elliptical, high-arched, with the apex strongly curved forward and downward, sometimes almost at the anterior end. The surface is smooth, or occasionally weakly radially ridged. Colour pale-olive to brownish, the apex coppery; inside silvery iridescent to reddish bronze. The species live mostly attached to large seaweeds, and range from southern Chile and Argentina to the Kerguelen Island.

Synonymy—

- 1817 *Nacella* Schumacher, Essai d'un Nouveau Systeme des Habitations, p. 179. Type, by subsequent designation, Gray, 1847: *Patella mytilina* Helbling, 1779.

Nacella mytilina (Helbling, 1779)

(Pl. 73, fig. 9; Pls. 173, 174)

Range—Southern Chile, Straits of Magellan, Tierra del Fuego, Falkland Islands and Kerguelen Island.

Description—Shell rather small, up to 43 mm. (1½ inches) in length, elliptical, thin and fragile, with the apex almost at the anterior end. Usually the surface is almost smooth, but occasionally moderate radial ridges are developed, as well as corrugations around the anterior margin. Colour greenish olive to light brownish, sometimes reddish bronze at the apex, and the interior is silvery iridescent.

Measurements (mm.)—(all A.W.B. Powell collection).

length	width	height
43.0	26.0	18.0
34.5	23.0	11.0
27.0	18.0	7.5

Punta Arenas
Falkland Islands
Hermit Id., Cape Horn

Synonymy—

- 1779 *Patella mytilina* Helbling, Abh. Privatges. Bohm., vol. 4, p. 104, pl. 1, figs. 5, 6.
1786 *Patella mytiliformis* Lightfoot, Cat. Portland Mus., p. 42.
1791 *Patella conchacea* Gmelin, Syst. Nat. ed. 13, p. 3708.
1817 *Nacella mytiloides* Schumacher, Essai Vers test., p. 179.
1819 *Patella cymbularia* Lamarck, Anim. sans Vert., vol. 6, p. 335.
1831 *Patella cymbuloides* Lesson, Voy. de la Coquille, p. 422.
1845 *Patella hyalina* Philippi, Arch. f. Naturg., vol. 11, p. 59.
1845 *Patella cymbium* Philippi, Arch. f. Naturg., vol. 11, p. 60.
1845 *Patella vitrea* Philippi, Arch. f. Naturg., vol. 11, p. 60.
1869 *Nacella compressa* Rochebrune & Mabille, Mission scient. Cap Horn, vol. 6, p. 98, pl. 5, fig. 9.
1913 *Nacella falklandica* Preston, Ann. Mag. Nat. Hist., ser. 8, vol. 11, p. 221, pl. 4, fig. 6.
1950 *Nacella mytilina* Helbling, Carcelles, Anales del Museo Nahuel Huapi, vol. 2, p. 52 (Kerguelen).
1951 *Nacella mytilina* Helbling Powell, Discovery Rep., vol. 26, p. 80.

- 1964 *Nacella mytilina* Helbling, Dell, Rec. Domin. Mus., vol. 4, no. 20, p. 273.

Records—STRAITS OF MAGELLAN (type locality): Punta Arenas; St. Martin's Cove, Hermite Island, Cape Horn. PATAGONIA: mouth of Santa Cruz River. FALKLAND ISLANDS (all AWBP coll.). KERGUELEN ISLAND: Swain's Bay, intertidal and Antares Island, intertidal (BANZARE Sta. 48 and Sta. 61).

Nacella kerguelensis (E. A. Smith, 1877)

(Pl. 73, fig. 10; Pl. 173, figs. 3, 4)

Range—Kerguelen Island, Heard Island and Macquarie Island.

Remarks—Dell (1964) has shown that the young stages of this species have the form of typical *Nacella*, and that in the adult the apex has moved back from near the front margin to a sub-central position. These adults, however, retain the light build of *Nacella*. It is possible that some of the lighter built Magellanic species of *Patina* go through a *Nacella* stage also, but at present there is no evidence in support of this theory.

The Macquarie Island record is based upon four beach shells, and none have been recorded since from that locality, so it is assumed that the original specimens may have drifted there upon floating kelp.

Description—Shell thin and fragile, large, up to 80 mm. (3¼ inches) in length, broadly ovate, but decidedly narrowed anteriorly, rather everted, and with the apex varying between near the front margin in juveniles to a subcentral position in adults. Sculpture consisting of weak radial folds. Colour dark purplish-brown, with the apex reddish-bronze; internally completely dark bronzy reddish-brown.

Measurements (mm.)—

length	width	height
80.0	65.5	33.0
67.0	57.0	24.0
46.0	37.0	15.6

Heard Island: Dell, 1964
Royal Sound, Kerguelen
Royal Sound, Kerguelen

Synonymy—

- 1877 *Patella (Patinella) kerguelensis* E. A. Smith, Phil. Trans. Roy. Soc., London, vol. 168, p. 177, pl. 19, figs. 13, 13a. (Kerguelen Island).
1886 *Patella kerguelensis* Smith, Watson, Challenger Rep., vol. 15, p. 27.
1908 *Patinella kerguelensis* Smith, Strebel, Schwed. Sudpol. Exped., Zool., vol. 6, p. 83.
1916 *Nacella kerguelensis* Smith, Hedley, Aust. Ant. Exped. 1911-1914, ser. C, vol. 4, pt. 1, p. 44. Macquarie Island.
1957 *Patinigera kerguelensis* Smith, Powell, B.A.N.Z. Ant. Res. Exped., vol. 6, p. 126.
1964 *Nacella kerguelensis* Smith, Dell, Rec. Domin. Mus., vol. 4, no. 20, p. 276.

Subgenus *Patinigera* Dall, 1905

Type: *Patella magellanica* Gmelin, 1791

Shells of the subgenus are mostly more solid than those of typical *Nacella*. They have the apex well back from the anterior end, sometimes being subcentral in position. The interior is always with a bronze lustre. As in typical *Nacella*, the gill cordon is complete and there is a well-developed epipodial fringe. The radula shows no important differences.

The subgenus is more widely distributed than is typical *Nacella*. It extends up the western coast of South America as far as Valparaiso, and southward to the subantarctic islands and Antarctica. It also occurs at Macquarie Island, and reaches its furthest north location in the New Zealand faunal region at Campbell Island, 52° 33'S.

Synonymy—

- 1871 *Patinella* Dall, Proceedings of the Boston Society of Natural History, vol. 14, p. 53. Type by original designation: *Patella magellanica* Gmelin, 1791.
1905 *Patinigera* Dall, Nautilus, vol. 18, no. 10, nom. nov. pro *Patinella* Dall, 1871, non Gray, 1848.

Nacella clypeator (Lesson, 1831)

(Pl. 73, fig. 13; Pl. 175, figs. 1-2)

Range—Chile, to as far north as Valparaiso.

Remarks—The species is easily recognised by its nearly circular outline.

Description—Shell of moderate size, up to 61 mm. (2½ inches) in length, rather depressed and almost circular in outline, with the apex subcentral. Sculpture consisting of very numerous, regular, narrow, low rounded, radial ribs. Colour dull reddish-brown, the ribs paler; interior silvery to pale bronze, with the spatula area irregularly blotched with dark reddish-brown.

Measurements (mm.)—

length	width	height	
61.0	58.0	14.5	Chile; Pilsbry, 1891
56.5	51.0	17.0	Chile
47.0	43.5	14.5	Chile
37.0	32.0	9.0	Valparaiso

Synonymy—

- 1831 *Patella clypeator* Lesson, Voy. Coquille, Zool., vol. 2, p. 419.
1854 *Patella clypeator* Lesson, Reeve, Conch. Iconica, pl. 16, figs. 38 a, b. "Monterey, California," in error.
1891 *Nacella (Patinella) clypeator* Lesson, Pilsbry, Man. Conch., vol. 13, p. 122, pl. 50, figs. 40-43.

Nacella concinna (Strebel, 1908)

(Pl. 176, figs. 1-5)

Range—South Georgia, South Orkneys, South Shetlands, Bouvet Island, Seymour Island, Paulet Island, Wandel Island, Anvers Island and Petermann Island.

Remarks—Unfortunately the well-known name of this species, *Patella polaris* Hombron & Jacquinot, 1841, falls as a homonym of the same combination of Röding, 1798. However there is a substitute name available, in *Patinella polaris concinna* Strebel, 1908, from South Georgia, and this name, *concinna*, may be used specifically, since there appears to be no real difference between the shallow-water '*polaris*' and the deeper-water *concinna*, other than a gradual tendency towards lower profile, lighter build, more clear-

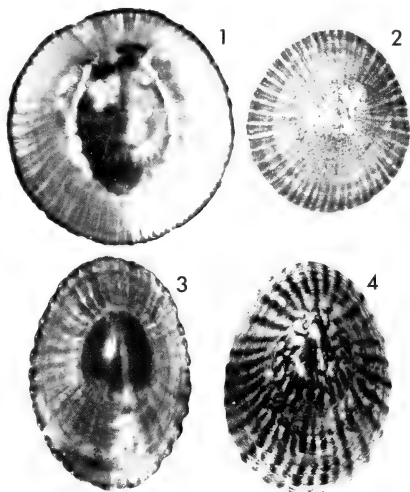


Plate 175. Figs. 1, 2, *Nacella (Patinigera) clypeator* (Lesson, 1831), Chile, 44-53 mm., AWBP coll. 46145. Figs. 3, 4, *Nacella (Patinigera) deaurata* (Gmelin, 1791), Falkland Islands, 60 mm., AWBP coll. 632.

cut ribbing and paler coloration as the depth increases. Strebel's *concinna*, described as a *Patinella*, does not conflict with the Japanese acmaeid that was originally described as *Patella concinna* Lischke. The species lives from the intertidal zone down to 110 metres.

Description (shallow-water 'polaris' form)—Shell moderately large, up to 60 mm. (2½ inches) in length, elongate ovate, rather thin, moderately elevated, with the apex between central and the anterior third. Sculptured with distant weak radial ribs in young shells, but the ribbing becomes subobsolete to obsolete in the adult. Colour, externally pale brownish; internally very

dark bronzy-brown, almost black, the spatula sometimes a paler chestnut-brown.

Description (deeper-water typical form)—Shell usually small, 20 to 32 mm. (¾ to 1¼ inches) in length, thin and fragile, elongate ovate, moderately elevated and with the apex at about the anterior third. Sculptured with about 28 to 30 narrow radial ribs, crossed by dense fine lamellose growth lines. Colour buff, sparingly blotched in reddish brown; interior cream, shining, varyingly maculated with pale reddish brown. Some larger examples, approaching the larger shallow-water form in size, tend to flatten out at the margin, towards which the radial sculpture becomes subobsolete.

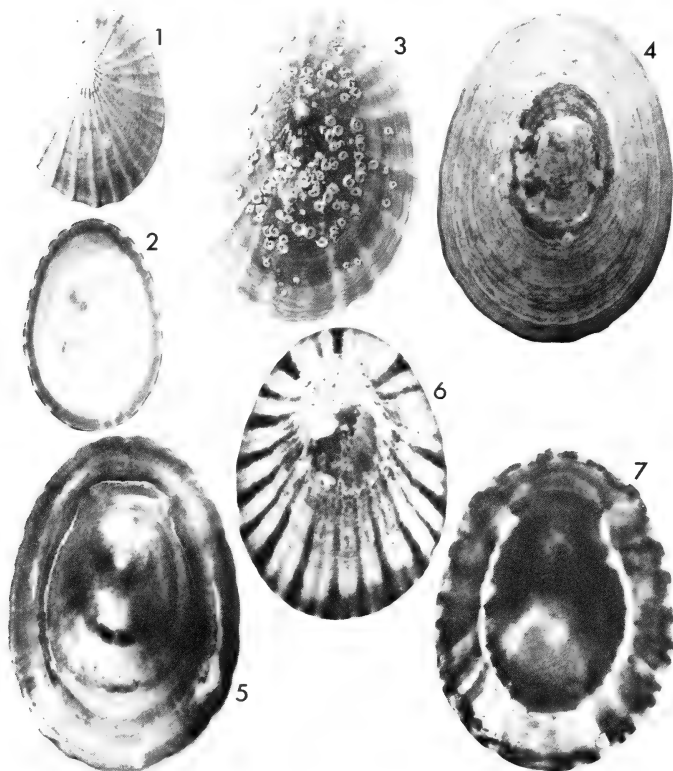


Plate 176. Figs. 1-5. *Nacella (Patinigera) concinna* (Strebel, 1908). Figs. 1, 2. (*concinna* form), East Cumberland Bay, South Georgia, 27 metres, 27 mm., AWBP coll. Fig. 3. East Cumberland Bay, 24-30 metres, 41 mm., AWBP coll. 26831. Figs. 4, 5. (*polaris* form), Melchior Island, Schollaert Channel,

Palmer Archipelago, 4-10 metres, 58 mm., AWBP coll. 52493. Figs. 6, 7. *Nacella (Patinigera) delesserti* (Philippi, 1849), Marion Island, south western Indian Ocean, 38-53 mm., AWBP coll. 52491.

Measurements (mm.)—

length	width	height	
58.0	42.0	19.0	Palmer Archipelago, 4-10 metres: (' <i>polaris</i> ' form)
44.0	31.0	18.5	S. Orkneys (' <i>polaris</i> ' form)
42.0	29.0	9.0	S. Georgia, 27 metres: (intermediate form)
31.0	21.5	11.0	S. Georgia (' <i>polaris</i> ' form)
29.0	20.0	8.0	S. Georgia, 18 metres: (typical <i>concinna</i>)
25.0	17.0	6.25	S. Georgia (typical <i>concinna</i>)

Synonymy—

- 1841 *Patella polaris* Hombron & Jacquinot, Ann. Sci. Nat. Zool., vol. 16, p. 191 (non Röding, 1798).
 1886 *Patella polaris* H. and J. Martens and Pfeffer, Moll. Süd-Georgien, J. hamb. wiss. Anst., vol. 3, p. 101, pl. 2, figs. 11-13.
 1891 *Nacella (Patinella) polaris* H. and J. Pilsbry, Man. Conch., vol. 13, p. 120, pl. 49, figs. 21-27.
 1908 *Patinella polaris* H. and J. Strebel, Wiss. Ergeb. schwed. Südpolar-Exped. (1901-3), vol. 6, p. 81, pl. 5, fig. 77.
 1908 *Patinella polaris concinna* Strobel, Wis. Ergeb. schwed. Südpolar-Exped. (1901-3), vol. 6, p. 82, pl. 5, figs. 76 a-e, 78 a, b.
 1951 *Patinigera polaris* H. and J. Powell, Discovery Rep., vol. 26, p. 82.
 1951 *Patinigera polaris concinna* Strebel, Powell, Discovery Rep., vol. 26, p. 83.

Records—SOUTH GEORGIA (type of '*polaris*'): Cumberland Bay, 15-25 metres (type of *concinna*); East Cumberland Bay, 18-110 metres; Moltke Harbour, in rock pool; Stromness Harbour, 26-35 metres; Undine Harbour, 18-27 metres. SOUTH ORKNEYS: Signy Island, 18-27 metres; Normanna Strait, 24-36 metres ('Discovery II'; Powell, 1951). SOUTH SHETLANDS: Deception Island, 5-60 metres; Nelson Island, shore; Livingston Island, shore; Wilhelmina Bay, Danco Land, 1-8 fathoms ('Discovery II'; Powell, 1951). PALMER ARCHIPELAGO: Melchior Island, 4-10 metres. Bouvet Island, 40-45 metres ('Discovery II'; Powell, 1951). Seymour, Paulet, Wandel, Anvers and Petermann Islands (Strebel, 1908; Lamy, 1911).

***Nacella deaurata subspecies deaurata*
(Gmelin, 1791)**

(Pl. 73, fig. 11; Pls. 174, 175)

Range—Southern Patagonia, Straits of Magellan, Tierra del Fuego and Falkland Islands.

Remarks—The species is nearest allied to *magellanica* which is more broadly ovate in outline and lacks nodulation of the radials.

Description—Shell of moderate size, up to 61 mm. (2½ inches) in length, rather solid, tall conical, narrowly ovate, and with the apex at about the anterior third. Sculpture consisting of from 36 to 40 strong radial ribs, which are rendered strongly scabrous to nodular by numerous overriding concentric lamellae. Colour yellowish-brown to reddish-brown, tending dark reddish-brown to bronze over the apical area.

Interior silvery with a pinkish lustre, more or less rayed and mottled with reddish-bronze, the spatula and spotted marginal border dark reddish-brown.

Measurements (mm.)—

length	width	height	
61.0	43.0	27.0	Falkland Islands
57.0	43.0	24.0	Falkland Islands
48.0	34.0	19.5	Falkland Islands

Synonymy—

- 1784 *Patella aenea* Martyn, Univ. Conch., vol. 1, fig. 17 (invalid).
 1791 *Patella deaurata* Gmelin, Syst. Nat. ed. 13, p. 3719, based upon Martini-Chemnitz, Conch. Cab., vol. 10, p. 327, pl. 168, figs. 1616 a, b.
 1854 *Patella varicosa* Reeve, Conch. Iconica, pl. 11, figs. 21 a-c.
 1885 *Nacella strigatella* Rochebrune and Mabilie, Bull. Soc. Phil. Paris, ser. 7, vol. 9, p. 110.
 1891 *Nacella (Patinella) aenea* Martyn, Pilsbry, Man. Conch. vol. 13, p. 118, pl. 46, figs. 28-36.
 1913 *Helcioniscus bennetti* Preston, Ann. Mag. Nat. Hist. ser. 8, vol. 11, p. 221, pl. 4, fig. 7.
 1951 *Patinigera aenea* Martyn, Powell, Discovery Rep. vol. 26, p. 82.

***Nacella deaurata form delicatissima*
(Strebel, 1907)**

(Pl. 178, figs. 3, 4)

Range—Straits of Magellan and Falkland Islands.

Remarks—This is a small thin shell of low profile with delicately squamose ribs, and of pale colour with a few rays and streaks of reddish-brown at most. The writer has insufficient material to properly evaluate this shell which may prove to grade into the typical species. It occurs from 5 to 50 fathoms.

Measurements (mm.)—

length	width	height	
46.7	36.9	15.8	Strebel, 1908, pl. 5, fig. 75
21.4	16.6	5.7	Strebel, 1908, p. 145.
15.0	10.75	3.25	Eddystone Rock, Falklands, 115 metres

Synonymy—

- 1907 *Patinella delicatissima* Strebel, Zool. Jahrb. Abt. Syst., Jena, vol. 25, p. 145, pl. 5, figs. 71, 72, 74, 75.
 1908 *Patinella delicatissima* Strebel, Wiss. Ergeb. schwed. Südpolar-Exped., vol. 6, pt. 1, pl. 1, figs. 75, 75a.
 1951 *Patinigera delicatissima* Strebel, Powell, Discovery Rep., vol. 26, p. 82.

Records—STRAITS OF MAGELLAN: 20-30 fathoms (type locality); Ushuaia, Tierra del Fuego, 1-2 fathoms (Strebel, 1908). FALKLAND ISLANDS: off Eddystone Rock, East Falkland Islands, 115 metres; entrance to Port Stanley, 10-16 metres; Sparrow Cove, Port William, 10.5-16 metres (Discovery 11, Sta. 51, 52 and 56).

***Nacella delesserti* (Philippi, 1849)**

(Pl. 176, figs. 6, 7)

Range—Marion Island (between South Africa and Antarctica).

Remarks—The writer has only two examples of this species available but they seem to represent a distinct species, characterised by an elongate ovate outline and simplicity of both sculpture and colour pattern. According to Hedley (1916, Aust. Ant. Exped., ser. C, vol. 4, pp. 42, 43) *delesserti* was based upon an immature shell of only 22 mm. in length. Reeve (1854, *Conch. Iconica*, sp. 40, pl. 17) named a shell from unknown locality, *Patella ferruginea*, basing it apparently, upon a manuscript species of Sowerby, and with *Patella delesserti* Philippi cited in its synonymy. However Reeve's figures are unlike any shell I have seen and certainly bear no resemblance to the Marion Island limpet.

Description—Shell of moderate size, up to 54 mm. (2½ inches) in length, elongate ovate, more narrowly rounded anteriorly and of moderate elevation, with the apex between the anterior

third and fourth. Sculpture consisting of about 24 low, carinated to rounded, radial folds and an occasional intermediate, the whole surface densely crossed by weak lamellose growth lines. Colour of exterior greyish-white, with most of the primary radials dark reddish-brown. Interior heavily blotched and radially streaked in dark reddish-bronze. Spatula very large.

Measurements (mm.)—

length	width	height	
53.0	40.0	16.0	Marion Island
38.0	27.5	13.0	Marion Island

Synonymy—

1849 *Patella delesserti* Philippi, *Abbild. Conch.* vol. 3, pt. 4, p. 9, pl. 1, fig. 5.

***Nacella edgari* (Powell, 1957)**

(Pl. 177, figs. 3, 4; pl. 179)

Range—Kerguelen Island.

Remarks—The adult shell is very thin and fragile, almost flat to slightly concave, with an animal too large to allow the shell tight contact with the surface of the kelp. Young examples sometimes occur on rocks, and such have a slight elevation, as well as crisp narrow radials, but these become

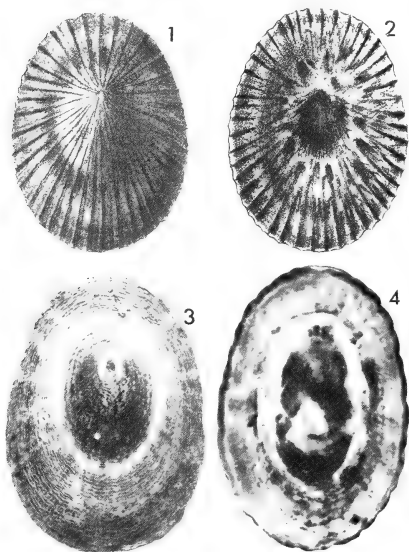


Plate 177. Figs. 1, 2, *Nacella (Patinigera) fuegiensis* (Reeve, 1855), "Tierra del Fuego, Falkland Islands", from Reeve, 1855, pl. 28, fig. 73. Figs. 3, 4, *Nacella (Patinigera) edgari* (Powell, 1957), Royal Sound, Kerguelen Island, in fish trap, 34 mm., AWBP coll.

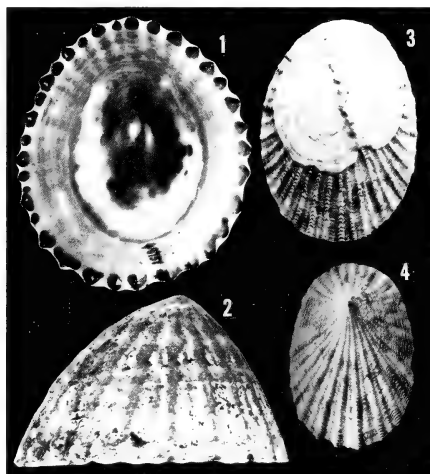


Plate 178. Figs. 1, 2, *Nacella (Patinigera) magellanica* (Gmelin, 1791), Straits of Magellan, 51 mm., AWBP coll. 48751). Figs. 3, 4, *Nacella (Patinigera) deaurata* subspecies *delicatissima* (Strebel, 1907), Falkland Islands, 115 metres, 16 mm., AWBP coll.

subobsolete as the shell grows and flattens out at the edges. It is associated with kelp from intertidal to about 55 metres.

Description—Shell elongate-ovate, of moderate size, up to 51 mm. (2 inches) in length, very thin and fragile, and very depressed, only the apical area slightly raised, and much of the remaining dorsal surface actually concave. Sculpture consisting of many radial folds, that are narrow at first but soon become broad and low, almost disappearing towards the margin in adults. The whole surface crowded with sharp concentric lamellae that undulate as they cross the radials. Colour dull-slate externally, tinged with bronze at the apex; internally, iridescent bluish grey, with the spatula and an irregular marginal border diffused reddish brown.

Measurements (mm.)—(All station numbers are of the British, Australian and New Zealand Antarctic Research Expedition, 1929-1931).

length	width	height	
51.0	33.0	8.0	holotype; Royal Sound, 20 metres. Sta. 5
43.0	30.5	3.5	Colbeck Passage, 20 metres. Sta. 55a.
40.0	27.5	4.5	Royal Sound, 1-5 metres. Sta. 55b.
38.0	26.5	10.5	Swain's Bay, intertidal. Sta. 48.

Synonymy—

- 1877 *Patella (Patinella) fuegiensis* Reeve, E. A. Smith, Phil. Trans. Roy. Soc. London for 1879 (issued separately 1877), vol. 168, p. 180, pl. 9, figs. 14, 14a. Not Reeve, 1855.
 1891 *Nacella (Patinella) fuegiensis* Reeve, Pilsbry, Man. Conch. vol. 13, p. 121 (in part, pl. 49, figs. 28, 29 only). Not Reeve, 1855.
 1957 *Patinigera fuegiensis edgari* Powell, B.A.N.Z. Ant. Res. Exped., vol. 6, pt. 7, p. 127, text figs. 1, 1a, 1b.

Types—The holotype and paratypes are at present in the Auckland Museum.

Records—KERGUELEN ISLAND, thirteen B.A.N.Z.A.R.E. Stations from in and around Royal Sound, ranging from low tide to 55 metres. The type locality is Port Jeanne d'Arc, Royal Sound, 20 metres, along the lower edge of the kelp belt.



Plate 179. *Nacella (Patinigera) edgari* (Powell, 1957). Grotto Bay, Port Jeanne d'Arc, Kerguelen Island, 10 metres, 37.5 x 25.5 x 4 mm. In profile to show the very slight elevation of the shell.

Nacella flammæa (Gmelin, 1791)

(Pl. 181)

Range—Straits of Magellan.

Remarks—This shell resembles *fuegiensis* in its narrowly oval outline, moderate elevation, and light build, but differs in sculpture, the radials being almost obsolete, represented at most by broad very weak radial folds towards the margin. The colour pattern is of broad irregular axial streaks upon a whitish ground.

Description—Shell elongate-ovate, of light build, and of moderate size, up to 40 mm. (1½ inches) in length, moderately elevated, and with the apex at between the anterior third and fourth. Surface relatively smooth, just a few, almost obsolete, broad low radial folds over the posterior half of the shell, and only towards the outer margin. The only other sculpture consists of very faint concentric growth lines. External colour pattern of broad, flexuous, dark reddish brown axial streaks upon a whitish ground; internally, the colour pattern is the same, except for a bright chestnut spatula.

Measurements (mm.)—

length	width	height	
39.0	27.8	10.0	Strebel, 1907, p. 145
33.5	24.0	9.5	St. of Magellan
27.0	18.7	7.0	St. of Magellan

Synonymy—

- 1791 *Patella flammæa* Gmelin, Syst. Nat., ed. 13, p. 3716; based upon Martini-Chemnitz, Conch. Cab., 1, pl. 5, fig. 42.
 1907 *Patinella flammæa*: Strebel, Zool. Jahrb., 25 (1), p. 145, pl. 5, fig. 73.

Nacella fuegiensis (Reeve, 1855)

(Pl. 177, figs. 1, 2)

Range—Tierra del Fuego, Falkland Islands, Petermann Island and South Georgia.

Remarks—This is a thin-shelled, elongate-ovate species, with numerous, weak, almost smooth, radial ribs. It is of pale greenish ground colour, partially to almost entirely blotched with bronzy reddish brown. The somewhat similar *deaurata* is of stouter build and has the radials strongly scabrous.

Description—Shell elongate-ovate, of moderate size, up to 50 mm. (2 inches) in length, thin and fragile, moderately elevated and slightly laterally compressed. Sculpture consisting of numerous, narrow, sharply raised radials, in early stages of growth, but these tend to become broader and

lower towards maturity; the whole crossed by very dense sharp concentric lirae. Colour greenish grey, more or less blotched with reddish brown, and the apical area with a bronze lustre. Interior iridescent bronzy-brown, rayed with darker brown, corresponding to the external sculptural interspaces.

Synonymy—

- 1855 *Patella fuegiensis* Reeve, *Conch. Iconica*, pl. 28, figs. 73 a, b.
 1891 *Nacella* (*Patinella*) *fuegiensis* Reeve, *Pilsbry, Man. Conch.*, vol. 13, p. 121, pl. 49, figs. 30, 31 (non figs. 28, 29).

Nacella magellanica subspecies magellanica
 (Gmelin, 1791)

(Pl. 73, figs. 14, 15; Pl. 178, figs. 1, 2)

Range—Tierra del Fuego, Straits of Magellan, Patagonia and Falkland Islands.

Remarks—This is the common limpet of the Magellanic Region, and it is easily recognised by its roundly oval shape, high-conical profile, nearly central apex, and strong unsculptured radial ribbing.

Description—Shell of moderate size, up to 65.6 mm. (2½ inches) in length, rather solid, roundly ovate and high-conical, with the apex erect and near central, strongly and regularly sculptured with relatively few bold rounded radials that do not render the radials either scabrous or beaded. Colour of exterior variable, pale reddish brown to greenish grey or brown, occasionally with broad dark-brown radial bands. Interior metallic-brown or leaden with the spatula bronzy-chestnut, and either a continuous or spotted marginal border of very dark-brown, the brown spots, when present, corresponding to the external ribs.

Measurements (mm.)—

length	width	height	
65.6	58.3	41.5	Strebel, 1907, fig. 94a
53.5	45.5	31.0	Straits of Magellan
45.0	37.5	21.5	Punta Arenas
33.0	27.0	18.0	Straits of Magellan
26.0	21.0	13.5	Straits of Magellan

Synonymy—

- 1791 *Patella magellanica* Gmelin, *Syst. Nat.* ed. 13, p. 3703, based upon Gault, pl. 9, fig. E, and Martini-Chernitz, *Conch. Cab.* vol. 1, pl. 5, figs. 40 a, b.
 1854 *Patella magellanica* Gmelin, Reeve, *Conch. Iconica*, pl. 10, figs. 19 a, b.
 1854 *Patella atramentosa* Reeve, *Conch. Iconica*, pl. 17, figs. 41 a, b.
 1885 *Patella meridionalis* Rochebrune and Mabilie, *Bull. Soc. Phil.*, Paris, ser. 7, vol. 9, p. 109.

- 1885 *Patella metallica* Rochebrune and Mabilie, *Bull. Soc. Phil.*, Paris, ser. 7, vol. 9, p. 109.
 1885 *Patella pupillata* Rochebrune and Mabilie, *Bull. Soc. Phil.*, Paris, ser. 7, vol. 9, p. 110.
 1885 *Patella tincta* Rochebrune and Mabilie, *Bull. Soc. Phil.*, Paris, ser. 7, vol. 9, p. 110.
 1891 *Patinella aenea* var. *magellanica* Gmelin, *Pilsbry, Man. Conch.*, vol. 13, p. 119, pl. 44, figs. 9-17; pl. 43, figs. 1-6.
 1907 *Patinella magellanica-atramentosa* Strebel, *Zool. Jahrb. Abt. Syst. Jena*, vol. 25, p. 146, pl. 6, figs. 86-88; pl. 7, figs. 91, 92, 94, 95.
 1907 *Patinella aenea* var. *minor* Strebel, *Zool. Jahrb. Abt. Syst. Jena*, vol. 25, p. 137, pl. 5, figs. 67 a-d.
 1951 *Patinigera magellanica* Gmelin, Powell, *Discovery Rep.*, vol. 26, p. 81.

Nacella magellanica subspecies venosa (Reeve, 1854)

(Pl. 180, figs. 1-4)

Range—Chiloe Island, Chile.

Remarks—Both *venosa* and *chiloensis*, from the same locality, Chiloe Island, appear to represent but one form, a roundly ovate, high-conical, thin-shelled, sub-obsolete sculptured variant of *magellanica*, which, as suggested by Dell (l.c., 1964) may be a regional subspecies. Unfortunately the writer has no material available upon which to make further comment.

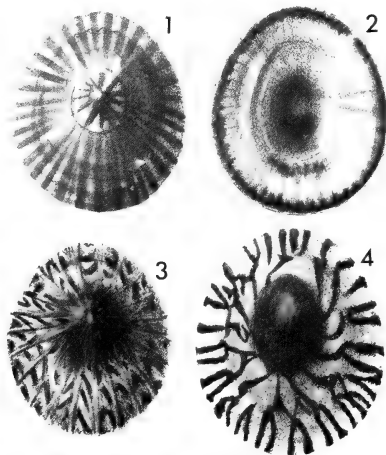


Plate 180. *Nacella* (*Patinigera*) *magellanica* subspecies *venosa* (Reeve, 1854) Chiloe Island, Chile. Figs. 1, 2. *Patella venosa* Reeve, 1854, *Conch. Iconica*, pl. 10, figs. 18 a, b. Figs. 3, 4. *Patella chiloensis* Reeve, 1855, *Conch. Iconica*, pl. 33, figs. 98 a, b.

Description—(original, for *venosa*) "Shell ovate, convex, rather high with age, a little contracted in front, in the young shell radiately ribbed, ribs small, rather distant, more or less obsolete with age, varicose near the margin; transparent-white, irregularly veined with chestnut-purple, veins bifurcated at the margin, deeply stained with purple-chestnut in the interior." Reeve's *chiloensis* is essentially similar in shape, height, sculpture and position of the apex, but differs in coloration, a minor point, in being irregularly stained and streaked in smoky-black.

Synonymy—

- 1854 *Patella venosa* Reeve, Conch. Iconica, pl. 10, figs. 18 a-c.
 1855 *Patella chiloensis* Reeve, Conch. Iconica, pl. 33, figs. 98 a, b.
 1964 *Patinigera magellanica venosa* Reeve, Dell, Rec. Domin. Mus., vol. 4, no. 20, p. 273.

Nacella macquariensis Finlay, 1927

(Pl. 182, figs. 1, 2)

Range—Macquarie and Heard Islands.

Remarks—Compared with *terroris*, *macquariensis* varies greatly both in outline and in height; also it has fewer and stronger primary radials, a tendency to be longer and narrower, and the spatula is always clearly defined, often heavily callused. In *terroris* the shape is constantly broadly ovate and the spatula is never clearly defined.

Description—Shell moderately large, up to 63 mm. (2½ inches) in length, strong but of light build, mostly narrowly ovate and elevated, but varying to rather broadly ovate and depressed. Sculpture consisting of from 32 to 35 broadly rounded primary radial ribs, plus narrower secondary intermediate radials, mostly over the posterior half of the shell; the whole surface crowded with low concentric growth lamellae, that do not thicken to any extent on the crests of the radials. Colour, externally, olive to chestnut-brown; internally, diffused and strongly rayed in bronzy reddish brown, the spatula well-marked, variously blotched with reddish brown, and often almost completely white-callused.

Measurements (mm.)—

length	width	height	
63.0	51.9	31.2	Garden Cove; Dell, 1964
58.0	46.0	22.0	Macquarie Island
43.0	33.0	14.0	Hurd Point
41.0	35.0	17.0	Hurd Point
41.0	30.0	12.5	Hurd Point

Synonymy—

- 1913 *Nacella fuegiensis* Reeve, Suter (in part), Man. N. Z. Moll., p. 77. Not Reeve, 1855.
 1916 *Nacella delesserti* Philippi, Hedley, Aust. Ant. Exped., ser. C, vol. 4, pt. 1, p. 42, pl. 6, figs. 65-69. Not Philippi, 1849.
 1927 *Nacella macquariensis* Finlay, Trans. N. Z. Inst., vol. 57, p. 337.
 1955 *Patinigera macquariensis* Finlay, Dell, Rec. Domin. Mus., vol. 4, no. 20, p. 274.

Types—The type series, based upon Hedley's 1916 figures (pl. 6, figs. 65-69), is in the Australian Museum, Sydney.

Records—MACQUARIE ISLAND (AWBP coll.); Hurd Point (AWBP coll.); Aerial Cove and Garden Cove (Dell, 1964). HEARD ISLAND: Atlas Cove and Cape Gazert (Dell, 1964).

Nacella terroris (Filhol, 1880)

(Pl. 73, fig. 12; Pls. 174, 182)

Range—Campbell Island, only, New Zealand subantarctic.

Remarks—This species marks the furthest north attained by this cold water genus in the New Zealand area, the latitude of Campbell Island being 52° 33' S. It is also interesting that at this same location, *Cellana strigilis* is abundant, in turn marking the most southerly occurrence of that warm water Indo-Pacific genus.

Description—Shell moderately large, up to 57 mm. (2¼ inches) in length, strong but of light build, rather broadly ovate, and high-conical, with the apex at about the anterior third. Sculpture consisting of about 50 narrow radial ribs, about 40 of them primary, the remaining ones being short and interpolated around the posterior margin. The whole surface is crossed by dense, crisp, undulating concentric growth lamellae,

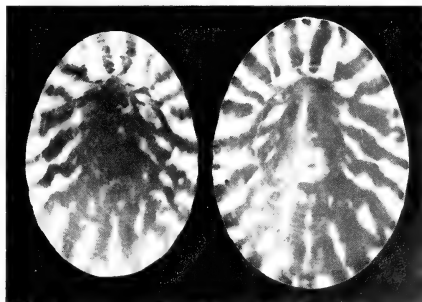


Plate 181. *Nacella (Patinigera) flammea* (Gmelin, 1791). Straits of Magellan, 27 mm. & 33.5 mm., AWBP coll. 46064.

that thicken where they cross the radials. Colour of exterior reddish to greenish-brown, without markings; interior, pale purplish grey, densely radiately lined in reddish-purple, and with irregular blotches of bronzy reddish brown over the central area, which lacks a clearly defined spatula.

Animal—As in other members of the genus, there is a prominent scalloped epipodial fringe that lies between the edge of the foot and the branchial cordon. This epipodial fringe is interrupted by the head but the branchial cordon is not.

Radula—Formula $3 + 1 + (1+0+1) + 1 + 3$. Moderately long and loosely coiled, in several volutions, on the right hand side of the animal, when viewed from above. This feature recalls the radula of *Cellana*, except that in that genus it is still longer and has more coils.

Measurements (mm.)—(all A. W. B. Powell, coll.).

length	width	height	
50.0	39.0	24.0	Perseverance Harbour
57.0	46.5	27.0	Perseverance Harbour
46.0	36.0	15.0	Perseverance Harbour
39.0	31.5	17.0	Perseverance Harbour
33.25	26.75	15.0	Perseverance Harbour

Synonymy—

1880 *Patella terroris* Filhol, Compt. Rend., vol. 91, p. 1095.

1885 *Patella terroris*: Filhol, Mission l'Île Campbell, p. 529.

1913 *Nacella (Patinigera) illuminata* (non Gould): Suter (in part), Man. N. Z. Moll., p. 77.

1955 *Patinigera terroris*: Powell, D.S.I.R. Cape Exped. Ser., Bull. 15, p. 69.

Types—The type specimens are in the Muséum National d'Histoire Naturelle, Paris.

Records—CAMPBELL ISLAND (type), New Zealand subantarctic: Perseverance Harbour, on rocks at low tide (Auck. Mus.; AWBP coll.).

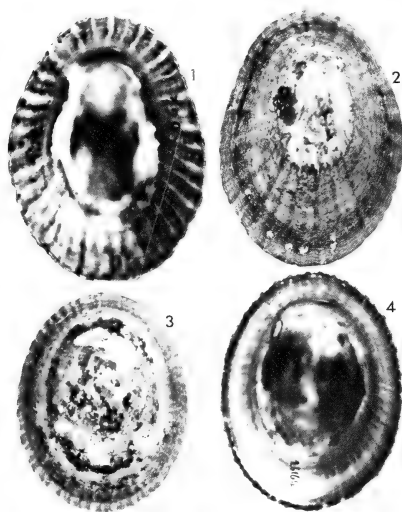


Plate 182. Figs. 1, 2. *Nacella (Patinigera) macquariensis* Finlay, 1927, Hurd Point, Macquarie Island, 40 mm., AWBP coll. 42864. Figs. 3, 4. *Nacella (Patinigera) terroris* (Filhol, 1880), Perseverance Harbour, Campbell Island, 52 mm., AWBP coll. 26164.

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Scutellastra H. and A. Adams, 123	01-649	turbator Iredale, 169	01-723
secernenda Dautzenberg, 95	01-579		
silicina Röding, 99	01-583		
sitta de Gregorio, 96	01-580		
solida Blainville, 171	01-725		
sontica Iredale, 170	01-724	umbella Gmelin, 119	01-637
sowerbyi Turton, 125	01-651	undato-lirata Reeve, 165	01-719
spectabilis Dunker, 84	01-560	ustulata Reeve, 137	01-661
spinifera Lamarck, 125	01-651		
squamata Röding, 96	01-580		
squamifera Reeve, 137	01-661	variabilis Krauss, 104	01-598
squamosa Gmelin, Turton, 126	01-652	varicosa Reeve, 195	01-763
stearnsii Pilsbry, 160	01-714	variegata Blainville, 170	01-724
stellaeformis Reeve, 130	01-654	variegata Reeve, 148	01-702
stellata Bucquoy, Dautzenberg & Dollfus, 99	01-583	variegata Reeve (1842), 150	01-704
stellifera Gmelin, 182	01-736	venosa Reeve, 198	01-766
stellularia Quoy & Gaimard, 183	01-737	vidua Reeve, 116	01-630
strigatella Rochebrune & Mabilie, 195	01-763	vitiensis Powell, 158	01-712
strigilis Hombron & Jacquinot, 183	01-737	vitrea Philippi, 192	01-756
subgranularis Blainville, 96	01-580	vulcanicus Oliver, 176	01-730
subplana Potiez & Michaud, 99	01-583	vulgata Linnaeus, 95	01-579
taberna Powell, n. sp., 190	01-744	watsoni Christiaens, 98	01-582
tabularis Krauss, 126	01-652	whitechurchi Turton, 125	01-651
tabitensis Pease, 167	01-721		
taitensis Röding, 166	01-720		
talcosa Gould, 166	01-720	zebra: Reeve, 136	01-660

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THE FAMILY HARPIDAE OF THE WORLD

by HARALD A. REHDER

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Introduction

The family Harpidae includes as their most dominant element the harp shells of the tropical seas. These striking and colorful shells have long been favorites with collectors, although because

of the paucity of species in the genus and the relative rarity of most of the species, they have not been as popular a group as the cowries, the cone shells, and the volutes.

They have, however, been the subject of iconographic treatment by numerous authors: Kiener (1835), Reeve (1843), Chenu (1853), Küster (1857), Sowerby (1860), Tryon (1883), and Maxwell Smith (1948). The only really critical study to date of the genus is that of Sutor (1877). Hedley (1911) published a short note updating the nomenclature of the species.



Plate 183. Above: *Harpa amouretta* Röding, showing head region with the inhalent siphon and the left tentacle with the eye at the base. Oahu, Hawaii. X 2. Photo by Olive Schoen-

berg. Below: *Harpa major* Röding, showing autotomized posterior portion of the foot. Nuku Hiva, Marquesas. X 1. Photo by Otis Imboden, National Geographic Society.

Family characters

The Harpidae is one of the seven families comprising the superfamily Volutacea (considering the Vasidae and Turbinellidae as distinct families) of the order Neogastropoda, and is usually placed near the Olividae and Turbinellidae. As a matter of fact, the subfamily Harpidae was once placed in the family Olividae, undoubtedly because of the similarities in the characters of the foot and propodium and the extent of the parietal callus.

The shell is characterized by possessing a large body whorl marked by more or less strong ribs, with the spiral sculpture, if present, of secondary importance. The protoconch in this small family is notable for the variety shown in its form and in the number of its whorls. These nuclear differences are used to separate the genera and subgenera, and are mentioned in the key (p. 000) and in the diagnoses of the supraspecific groups. For representations of the various types of protoconchs see our illustrations. The aperture varies from broadly to narrowly ovate; the parietal and columellar areas of the ventral side are covered by a callus of varying extent. The anterior siphonal sinus is well-marked, a siphonal canal is very short or absent, and there is generally a shallow posterior sinus at the junction of the outer lip and the parietal wall. An operculum is absent.

The living species of *Harpa* have a shell vividly ornamented with reddish brown and various shades of pink in more or less intricate patterns. The shells of *Austroharpa* are brightly colored, with or without spots, or their color pattern may be restricted to scattered spots.

According to Quoy and Gaimard (1832-35, vol. 2, p. 617), shells of the males are always narrower than those of females.

The foot of the animal is very large and fleshy, often with a rough, rugose surface, and is con-

spicuously divided into two parts. The propodium is broadly arcuate in front, terminating laterally in points that extend well beyond the width of the hind portion of the foot, or metapodium; the anterior margin may be shallowly scalloped and is sometimes more or less furrowed or grooved vertically. The propodium is joined by a broad neck to the metapodium which is elongately lanceolate, tapering posteriorward to a point, with its margins also gently and undulatingly scalloped.

The head, when the animal is active, is usually hidden beneath the anterior edge of the shell with only the tentacles and long inhalent siphon visible. The siphon protrudes through the siphonal notch, and the tentacles, when the animal is viewed from above, emerge from each side of the siphon. The tentacles are slender, pointed, and bear the eyes at the anterior end of a lateral enlargement above the base of the tentacles. From near the base of the head on the right side arises in males the elongate, tapering penis. In a specimen of *Harpa amouretta* from Nuku Hiva, Marquesas, I was able to see the rather long extruded part of the proboscis. In the Harpidae this organ is of the pleuremboche type, in which only the basal part is invaginable, withdrawing the distal portion into a sheath in the body cavity; this sheath is depicted by Quoy and Gaimard in one of their drawings.

All exposed parts of the animal are usually vividly mottled and flecked with various shades of brown or red, from deep chestnut brown to pale brown or reddish brown, and sprinkled with spots of bright yellow. The tentacles and inhalent siphon are irregularly ringed with chestnut brown and also spotted with yellow. The penis either is sprinkled with very fine spots of reddish brown or is without spots. According to Quoy and Gaimard the base of the foot is lightly spotted or

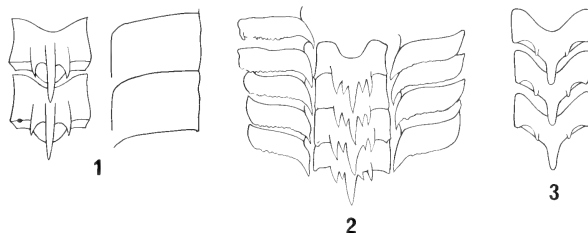


Plate 184. Radular teeth of: 1, *Harpa amouretta* Röding, X 600 (after Peile, 1939); 2, *Harpa amouretta* Röding, (after

Bergh, 1901); 3, *Harpa major* Röding, (after Troschel, 1866).

flecked with pale reddish brown. In preserved animals these colors first turn a more or less scarlet red and then usually fade.

The living animals and the anatomy of *Harpa major* and *H. amouretta* have been described and figured by Quoy and Gaimard (1832-35, vol. 2, pp. 611-620, pl. 42), and Bergh (1901) has published anatomical notes on *H. ventricosa*, *H. major*, *H. doris*, and *H. amouretta*. Earlier Reynaud had described the anatomy of either *major* or *davidis*, based on specimens from Ceylon (of which the shells are not described). His paper was read in 1829 but was published later (Reynaud, 1834); the figures in his paper are rather crude.

The radula of *Harpa* is very small, and Quoy and Gaimard were unable to find it in their examination of over twenty animals. Macdonald was apparently the first to discover the radula, which he said was "very minute compared with the whole bulk of the animal, as to appear quite rudimentary" (Macdonald, 1957, pp. 389-390). The radula was described and figured by Macdonald (1869, p. 116, pl. 13, fig. 14), and in the same year Troschel described that of *H. major* (Troschel and Thiele, 1866-93, p. 105, pl. 10, fig. 1). Troschel suggested the possibility that the radula teeth disappear in the adult stage, since the specimen of which he examined the radula was a juvenile. This probably accounts for Cooke's categorical statement that there is no radula in the adults of *Harpa* (Cooke, 1895, pp. 216, 221). Peile has figured and discussed the radula of *H. amouretta* (Peile, 1939, pp. 271-272) as has Bergh (1901, p. 625, pl. 47, fig. 21). For copies of some of these radula drawings, see plate 184. Attempts to extract the radula from a specimen of *Harpa costata* were finally successful, but in the process of staining and fixing, the radula became twisted on itself, and it was not possible to get a flattened

section of the radula. I was able, however, to confirm Peile's statement that the mesocone of the rachidian projects forward as a fang-like tooth. It appears that on each side of the mesocone is a single small cusp. On either side of the rachidian is a broad, segmented membrane that may, as Peile suggests, be the remains of the bases of lateral teeth.

Biology

Most of the living species of the genus *Harpa* live in moderately shallow to rather deep water where they progress over the sand or hard bottom and burrow in the sand by means of their large and strong foot. Reynaud (1834, p. 35) says that they move by using their propodium as a point of attachment and pull the rest of their body forward. I have not observed this in the living specimens I have seen, and other writers have not mentioned this means of progression.

Their mode of burrowing in the sand is described in a letter from Mrs. E. Coucaud of Port Louis, Mauritius. She observed *Harpa major* entering the sand with the shell perpendicular "until it was completely covered with sand. Then immediately by two or three successive movements I understood it had taken the horizontal position again, and then the tip of the siphon appeared from beneath the sand." Chabouis and Chabouis, in a natural history textbook for French Polynesia (Chabouis and Chabouis, 1954), say that after *H. major* has buried itself in the sand the only trace is a small hole in the center of a low mound which reveals the location of the siphon.

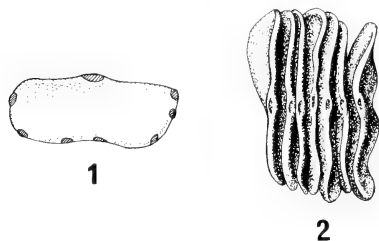


Plate 185. Egg capsules of *Harpa major* Röding from Ilot Tibarama, east coast of New Caledonia. 1, single egg capsule showing the "pore" at the top and 7 attachment scars; 2, view from top of cluster of egg capsules (after Risbec, 1932).

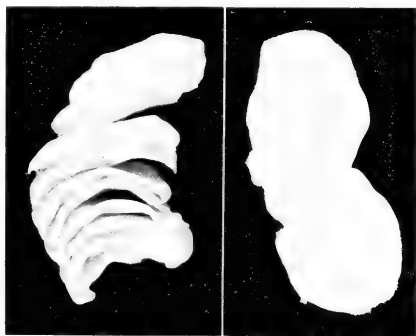


Plate 186. Egg mass of *Harpa amouretta* Röding from Batangas Province, Luzon Island, Philippines. Left fig. 11 capsules, about 40 mm. in width. Right fig., single capsule, showing pore at right, and broken attachment points at the left. Photo courtesy of R. Tucker Abbott.

An aspect of the behavior of species of the genus *Harpa* that has attracted the attention of even the older naturalists is that of autotomizing (self-amputation) the posterior portion of the foot when disturbed. Rumphius as early as 1705 mentions this habit. This trait, found also in some other genera of marine and land snails that possess a large foot, has been discussed at length by Quoy and Gaimard (op. cit.), Reynaud (op. cit.), and Jousseau (1883). Crichton (1941, p. 330) describes the autotomy of the hind portion of the foot of *H. davidis*, emphasizing the readiness with which this occurs. Several specimens of *H. major* dredged in the Marquesas severed the posterior portion of the foot (pl. 183), the severed ends of each part showing a clean edge (pers. obs. 1967). We did not notice any line of demarcation where the break occurred; Reynaud (op. cit.) states that there is such a line, but Quoy and Gaimard deny this.

Stasek (1967) has published a paper on autotomy in general, in which he cites the observations on *Harpa* by Quoy and Gaimard and Reynaud. In a recent article by Hardy (1972), autotomy in *H. ventricosa* and *amouretta* is described and figured.

None of the previous writers have published anything on the food of *Harpa*. Quoy and Gaimard state that they found nothing in the more than twenty stomachs of *Harpa* they examined, and believed that their food must be tenuous and readily assimilable. The first information on the feeding habits seems to be that of Chabouis and Chabouis (op. cit.). As this book, published in 1954, is not readily available, I give here a free translation of the pertinent paragraph:

"We have ascertained that the harp shell feeds on small crabs living in the sand, principally the box crab, *Calappa hepatica*, and the swimming crab, *Neptunus* [= *Portunus*] *sanguinolentus*. The anterior portion of the foot [propodium] holds the crab immobile on the substrate and the posterior portion [metapodium] glides underneath the crab, rolling itself around the imprisoned crab. At the same time the *Harpa* secretes a sticky fluid which combines with the sand to form a sort of a coating over the crab, asphyxiating it. We have seen a *Harpa* leave the sand while discarding the empty carapaces, probably after a meal."

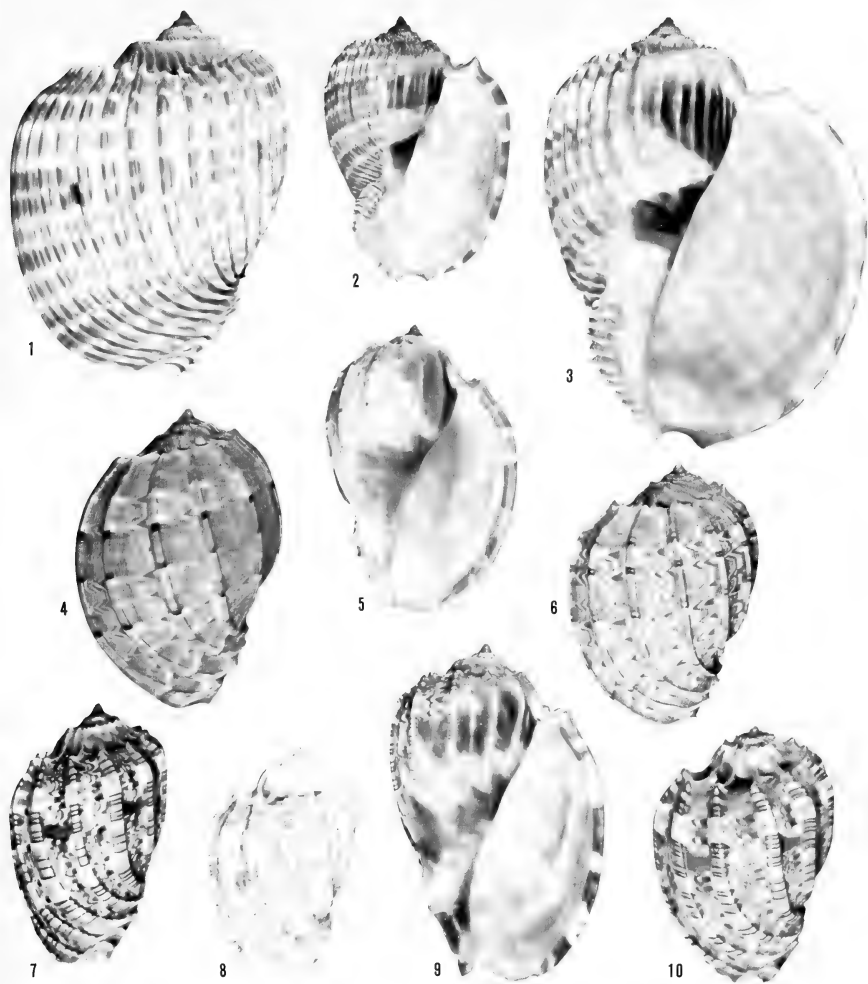
This observation is confirmed by Mrs. Coucaud in a letter from Mauritius in which she wrote that she has seen *Harpa major* "lying on one side with the animal rolled like a ball around a small crab or shrimp which it was surely eating. I do not remember having noticed this with *Harpa minor*, however."

It is possible that the mucus or some other secreted fluid contains a toxin that immobilizes or kills the crab on which the *Harpa* feeds. How the carapace and other hard parts of the crab are attacked by the snail in order to get at the soft parts is not known. The long proboscis is well suited to suck up the juices of the victim, the tiny radula possibly acting to reduce the larger pieces of flesh.

Harpa has several rather conspicuous mucus glands in the body cavity which can secrete large quantities of mucus when the animal is disturbed, as we discovered when picking out living specimens in the dredge hauls we made in the Marquesas. Quoy and Gaimard comment on the difficulties that the coagulated mucus caused during their dissection and examination of *Harpa major*.

The only literature reference to the eggs of *Harpa* that I have found is the note by Risbec on a female of *Harpa major* (he used the name *Harpa nabulum* Mart.) that he found in New Caledonia depositing eggs (Risbec, 1932, p. 368). The snail when discovered had not yet completed the task, and with her foot covered the whole egg mass which was attached to a rock. The ootheca are lamellar, rather tough, roughly rectangular in shape, about 30 mm. long and 15 mm. high, and irregularly attached to each other. The opening is in the center of the upper edge, and each capsule contained about three to four thousand yellowish white eggs. In shape the individual egg capsules are rather like those of certain species of *Busycon*, and when viewed from above the serially arranged capsules remind one of a portion of a *Turbinella* or a *Busycon* egg mass (Plate 185).

Dr. R. Tucker Abbott kindly examined and photographed for me the egg masses of *Harpa amouretta* Röding. The first egg mass (Plate 186) was laid by a female (typical shell form, Pl. 189, figs. 6-8) from Batangas Province, Luzon, Philippines, on March 25, 1965, and consisted of eleven lamellar, rather pliable, tough, rectangular ootheca, about 40 mm. in width and 20 mm. high. At the top of each capsule is a lanceolate pore with a thin membrane covering it. The pore and the continuing slit on each side offers a potential opening of 20 mm. in length. The capsules have 5 to 7 points of attachment to each other. The shell length of the female is 46.8 mm.; its width is 28.0 mm. The second egg mass also consisted of eleven capsules, but they were more arching in shape and only 25 to 30 mm. in width. They were laid on June 12, 1966, on Panay Island, Philippines, by a female whose shell size is 44.5 x 26.5 mm. Approximately 3,000 to 4,000 eggs were in each capsule. The egg capsules were collected

Plate 187. *Harpa* from the Indo-Pacific.

Figs. 1, 2, 3. *Harpa costata* (Linné, 1758). 1, Fouquet Id., Mauritius (ANSP 265220); 2, immature from Mahébourg reefs, Mauritius (Del. Mus. Nat. Hist. 12246); 3, La Morne, Mauritius (USNM 666304).

Figs. 4, 5, 6. *Harpa davidis* Röding, 1798. 4, Rameshwaram, southern India (USNM 290884); 5, Indian Ocean (USNM

700307); 6, Indian Ocean (Del. Mus. Nat. Hist. 12248).

Figs. 7-10. *Harpa harpa* (Linné, 1758). 7 and 8, Losap Id., Mortlocks, Caroline Ids. (Del. Mus. Nat. Hist. 37567); 9, Siasi, Sulu Archipelago, Philippines (USNM 612453); 10, Ryukyu Island (USNM 343465).

and preserved by the well-known collector, James E. Norton, now of Arizona.

Reynault has recently published on the characters and origins of the apyrene spermatozoa found in *Harpa amouretta* (Reynault, 1965).

Classification

Linné placed the two species of harp shells that he described in his genus *Buccinum*. The first to give these shells a distinct generic appellation was Röding, who in 1798 used the name *Harpa*, including in this genus six validly named species. Lamarck a year later independently created the genus *Harpa* for the same group.

The harp shells were first placed in a distinct family by Bronn, who in 1849 proposed the family Harpina (Bronn, 1849, p. 469), including in this family also the genus *Dolium*. Early classification systems generally assigned the genus *Harpa* to the family Buccinidae (Gray, 1847, p. 138; Woodward, 1851, p. 116). H. and A. Adams (1853-54, p. 116) put *Harpa* in the subfamily Harpinae of the family Dactylidae (= Olividae), probably on the basis of the similarity in the nature of the large foot, parietal callus, and the absence or small size of the operculum. In this arrangement they were followed by Gray (1857, p. 26). Chenu was the first to use the family name Harpidae in the modern sense (Chenu, 1859, p. 204), and was followed in this usage by all later workers.

The first person who appears to have published on the differences between the then known living and fossil species was Jousseume, who in a short paper (Jousseume, 1881) pointed out these differences and suggested using the name *Cithara* Klein for the recent species, and restricting the name *Harpa* Lamarck to the fossil species. As the type species of *Harpa* is the recent species *H. harpa* Linné, *Cithara* 'Klein' Jousseume, 1881, falls into the synonymy of *Harpa* Röding.

In 1883 Fischer (1880-87, p. 601) proposed *Eocithara* as a section of *Harpa* for the fossil species. He also included *Silia* Mayer, 1877, as a subgenus of *Harpa*; this group, however, should probably be placed in the Volutidae, as it was put with a query by Cossmann as a subgenus in *Cryptochorda*, which he assigned to the family Harpidae (Cossmann, 1899, p. 78); the latter genus is now generally placed in the Volutidae.

For many years *Eocithara* was used as a subgenus of *Harpa*; Wenz (1943, pp. 1309-1311) has four subgenera under *Harpa*—*Harpa s.s.*, *Eocithara*, *Marwickara* Laws, 1935, and *Austroharpa* Finlay, 1931. Most recent workers in New Zealand and Australia, however, consider *Austro-*

harpa and *Eocithara* as distinct genera, an arrangement I am following in this paper.

Distribution

The living species of Harpidae are found in the tropical and subtropical waters of the world, absent only from the western Atlantic.

Of the two groups found living today, the genus *Austroharpa*, subgenus *Palamharpa* is restricted to the warm-temperate waters of southern Australia, from the southernmost part of Queensland, around the southern coast, to the vicinity of Perth, Western Australia. All these species live in moderately deep water, in 20 to 100 fathoms, and are rather rare.

The genus *Harpa* includes the brightly colored, strongly ribbed harp shells well-known in collections. Of the ten recognized species eight are found in the Indo-Pacific region. Only two of these are widely distributed over much the entire region; these are *amouretta* and *major*. *Harpa harpa* is almost as widely spread, but is rare in the Indian Ocean, and is not found in Polynesia, its range reaching only to the Gilbert Islands in Micronesia and Tonga in eastern Melanesia.

Two species, *ventricosa* and *costata*, have a restricted distribution in the western Indian Ocean. *H. davidis* is found only in the eastern Indian Ocean, and *H. articularis* is restricted to the south-western Pacific Ocean. *Harpa gracilis* is a rare species found only in the coral atolls of the central Pacific, from the Ellice Islands to the Tuamotus and Clipperton Island.

The remaining two species of *Harpa* are found outside of the Indo-Pacific: *H. doris* along the West African coast and on Ascension Island, and *H. crenata* in the Panamic province.

Most of the species of *Harpa* are found in moderately deep water, and have been collected alive only by dredging, diving, or being found in fish traps. Only of *amouretta* have we definite knowledge of being found in shallow water and on reef flats; *gracilis* may also have a similar habitat.

Paleontological History

The earliest members of the family Harpidae belong to the genus *Eocithara*, of which eleven nominate species (one species has three subspecies) are known, and which has been found in Tertiary deposits from the Upper Paleocene to the Middle Miocene. The oldest species is *Eocithara morgani* Cossmann and Pissaro, 1909, from the Ranikot beds of the Upper Paleocene of Pakistan. A relatively recently discovered specimen

belonging to this genus in Lower Eocene beds of New Zealand is another bit of evidence that at this early period an arm of the Tethys Sea must have extended to New Zealand. We now know, therefore, that by Middle Eocene times the genus *Eocithara* had spread in the east to New Zealand, and to the westward as far as Texas and California. Upper Eocene species are known from Burma and Mississippi.

Regarding the phylogenetic origin of the Harpidae we are still in doubt as to a possible ancestral form, and to spend much time on this problem is to my mind an exercise in futility. Cox has outlined the situation very well when he wrote "Although the apparent great faunal gap between the Cretaceous and the Tertiary has diminished considerably with increased knowledge, it may still be said that we know nothing of the ancestry of most of the new molluscan groups that appeared during the period of intense evolutionary activity which marked the transition from Mesozoic to Cainozoic times . . . each new genus . . . appears more or less suddenly, without any evidence of having evolved gradually from older forms . . . the more we know, the more we are forced to the conclusion how incomplete the record is, and may always remain" (Cox, 1930, pp. 142-143).

If we cannot determine the origins of the Harpidae we can make some conjectures as to the later history of the family. It seems very possible that the family, along with other warm-water genera "first evolved in the Indian Ocean and subsequently migrated westwards" (Cox, loc. cit.). In Middle Eocene times the genus *Eocithara* is found in Texas and as far west as California where it is represented by a subspecies of *E. mutica* of the Paris Basin, as well as by a distinct species. Another species is found in the Upper Eocene of Mississippi.

To the east of India the genus persisted longer than in Europe, where its last representative is found in the Lower Oligocene. In Java a species of *Eocithara* is found in the Miocene, and in the Marshall Islands a fragment assignable to this genus has been found in beds of Upper Miocene age.

From ecitharid stock arose a species found in the Upper Eocene of New Zealand that has been placed in a distinct subgenus, *Marwickara* Laws, 1935. Another species, of quite different aspect but with a parallel origin, is found in the Middle Miocene of southern Australia; this is now placed in the subgenus *Refluharpa* Iredale, 1931.

Meanwhile a distinct group was arising, probably derived from some early ecitharid stock. This was the genus *Harpa*, characterized by a relatively smaller, broadly conical spire, a greater fusion and extension of the successive expanded upper portions of the outer lip and parietal callus over the preceding whorl, and a thinner, broader, not strongly marginate parietal and columellar callus that is more closely appressed over the ventral surface of the siphonal fasciole. One of the key differential characters is the multispiral, elevated-conical protoconch with peripherally keeled whorls found in *Harpa*; this contrasts with the paucispiral protoconch of *Eocithara* with its somewhat planate apex.

Unfortunately the protoconch of most of the specimens of fossil species assigned to *Harpa* is more or less eroded and thus the characters are not clear. Other characters, however, observed in certain fossil species, such as the nature of the parietal callus and its extension over parts of the penultimate whorl, have induced me to place them in the genus *Harpa* rather than in *Eocithara*.

The oldest recognized species of *Harpa* is *H. myrmia* Olsson of the Lower Oligocene of Peru. Other species are found in the Lower and Middle Miocene of France, Italy, the Caribbean, and Fiji, and in the Pliocene of Japan. From Miocene times onward species now living are represented in the fossil record.

In the Oligocene and Lower Miocene times there arose in southern Australia a stock of small fossil species which are now all placed in the genus *Austroharpa*. These are distinguished from both *Eocithara* and *Harpa* by their paucispiral, bulbous or dome-shaped protoconch. Their phylogenetic origin is unknown, but some of the Middle Miocene and Pliocene species gave rise to the four recent species that now live in the warm-temperate waters of southern Australia.

List of Recognized Taxa

The daggers (†) preceding the taxa indicate fossil forms.

Family Harpidae Bronn, 1849

GENUS *Eocithara* Fischer, 1883

Subgenus *Eocithara* Fischer, 1883

†*morgani* Cossmann and Pissaro, 1909. Upper Paleocene, Pakistan

†*mutica* Lamarck, 1803. **Type.** Middle Eocene, France

†subsp. *altavillensis* Defrance, 1821. Middle Eocene, France

†subsp. *hilarionis* Gregorio, 1880. Middle Eocene, northern Italy

†subsp. *californica* Vokes, 1937. Middle Eocene, California

†*clarki* Vokes, 1937. Middle Eocene, California

†*raricostata* Risso, 1826. Middle or Upper Eocene, France

†*elegans* Deshayes, 1835. Upper Eocene, France

†*jacksonensis* Harris, 1896. Upper Eocene, Mississippi

†*birmanica* Vredenburg, 1923. Upper Eocene, Burma

†*submutica* Orbigny, 1852. Lower Oligocene, France

†*narica* Vredenburg, 1925. Oligocene, Pakistan

†*bellardii* Sacco, 1890. Oligocene, Italy

†*muticaeformis* Martin, 1916. Lower Miocene, Java

Subgenus *Marwickara* Laws, 1935

†*waihaensis* Laws, 1935. **Type.** Upper Eocene, New Zealand

Subgenus *Refluharpa* Iredale, 1931

†*lamellifera* Tate, 1889. **Type.** Middle Miocene, southern Australia

GENUS *Harpa* Röding, 1798

harpa Linné, 1758. **Type.** Recent, Indo-Pacific

†*tosa* Aoki, 1966. Lower Pliocene, Japan

†*amouretta* Röding, 1798. †Pliocene to Recent, Indo-Pacific

gracilis Broderip and Sowerby, 1829. Recent, Micronesia and Polynesia

articularis Lamarck, 1822. †Upper Miocene to Recent, southwestern Pacific

major Röding, 1798. †Miocene to Recent, Indo-Pacific

davidis Röding, 1798. Recent, eastern Indian Ocean

ventricosa Lamarck, 1816. Recent, western Indian Ocean

costata Linné, 1758. Recent, islands of western Indian Ocean

doris Röding, 1798. Recent, west coast of Africa; Ascension Island

†*broichom* Cossmann, 1899. Lower Miocene, France

†*josephinae* Sacco, 1890. Middle Miocene, Italy

†*americana* Pilsbry, 1922. Middle Miocene, Caribbean

crenata Swainson, 1822. Recent, eastern Pacific

†*myrmia* Olsson, 1931. Lower Oligocene, Peru

GENUS *Austroharpa* Finlay, 1931

Subgenus *Austroharpa* Finlay, 1931

†*pulligera* (Tate, 1889). **Type.** Middle Miocene, southern Australia

Subgenus *Palamharpa* Iredale, 1931

exquisita (Iredale, 1931). **Type.** Recent, southeastern Australia

loisae Rehder, 1973. Recent, southern Western Australia

punctata (Verco, 1896). Recent, South Australia

wilsoni Rehder, 1973. Recent, southern Western Australia

†*sulcosa* (Tate, 1889). Middle Miocene, southern Australia

†*tatei* Finlay, 1931. Pliocene, South Australia

†*spirata* (Tate, 1889). Middle Miocene, Southern Australia

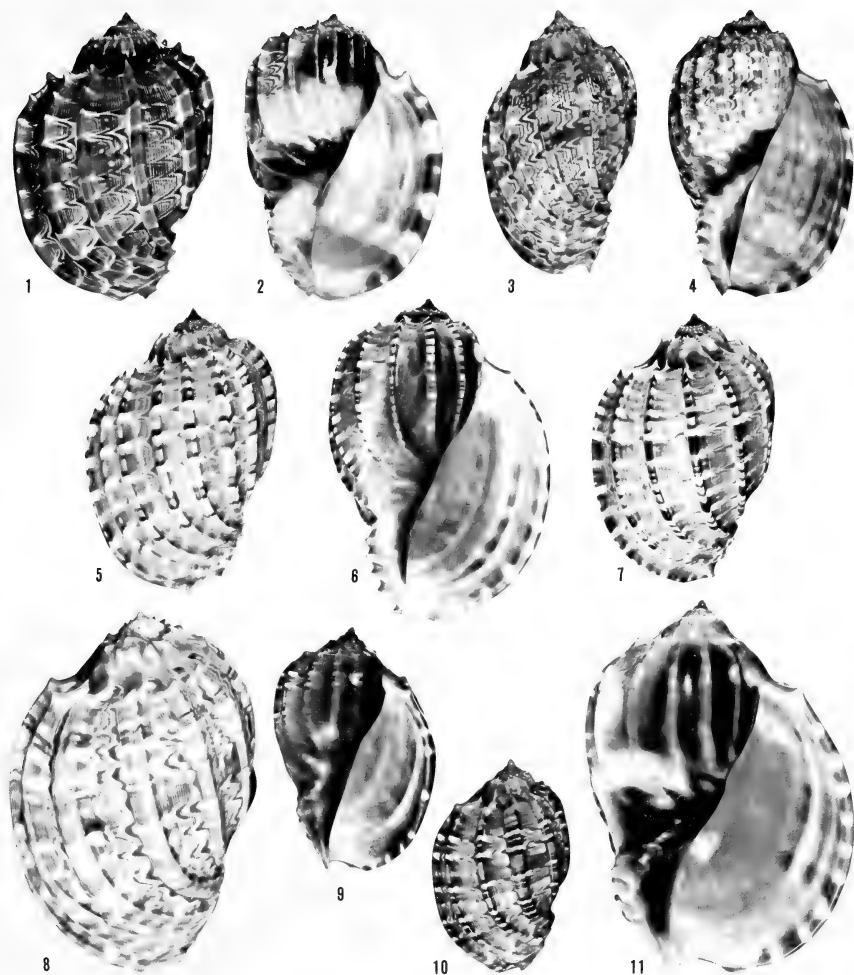
†*tenuis* (Tate, 1889). Lower to Middle Miocene, southern Australia

†*abbreviata* (Tate, 1889). Middle Miocene, southern Australia

†*clathrata* (Tate, 1889). Lower Miocene, southern Australia

†*pachycheila* (Tate, 1894). Upper Oligocene, southern Australia

†*cassinoides* (Tate, 1889). Pliocene, southern Australia

Plate 188. *Harpa* from the Indo-Pacific.

Figs. 1, 2. *Harpa ventricosa* Lamarck, 1816. 1, Zanzibar (USNM 597093); 2, Mauritius (USNM 666302).

Figs. 3, 4. *Harpa kajiyamai* Rehder, new species. 3, paratype from the Philippines; 4, holotype, Philippines (Nat. Sci. Mus. Tokyo 41450).

Figs. 5-7. *Harpa articularis* Lamarck, 1822. 5, off Taiwan

(USNM 681738); 6, Cebu, Philippines (USNM 612451); 7, southwest Pacific (Del. Mus. Nat. Hist. 1743).

Figs. 8-11. *Harpa major* Röding, 1798. 8 and 11, typical form from Cebu, Philippines (USNM 543683) and Okinawa, Ryukyu Ids. (USNM 670380); 9 and 10, dark form or forma *ligata* Menke (Australian Mus. C. 73513) from Melanesia.

Doubtful and erroneously assigned species

Harpa crescentensis Weaver and Palmer, 1922

Range—Middle Eocene of Washington (Crescent formation).

Remarks—This small species, the holotype measuring only 6 mm. in length, does not appear to be a true *Harpa*. The attenuate anterior end of the body whorl (the authors in their original description speak of the "canal moderately elongate") is unlike that found in any species of Harpidae, as is the relatively broad, high spire. Vokes (1937, p. 12, pl. 2, fig. 9) figures a supposed topotype, somewhat larger (9.3 mm.) than the type, which shows the broad high spire but the specimen has a more typically harpid aperture, without any narrowing at the siphonal canal. Possibly two species are involved here.

Synonymy—

1922 *Harpa crescentensis* Weaver and Palmer, Univ. Washington Publ. Geology, vol. 1, p. 40, pl. 11, fig. 21 (Port Crescent, Clallam Co., Washington).

1937 *Harpa?* *crescentensis* Weaver and Palmer, Vokes, Jour. Paleont., vol. 11, p. 12, pl. 2, fig. 9.

1942 *Harpa crescentensis* Weaver and Palmer, Weaver, Univ. Washington Publ. Geology, vol. 5, p. 498, pl. 95, figs. 12, 13.

Harpa dechordata White, 1888

Range—Paleocene of Brazil.

Remarks—This species, with broad rugose folds on only the upper half of the body whorl, has been placed in *Pseudoliva* (Olividae) by Harris (1896, p. 154).

Synonymy—

1888 *Harpa dechordata* White, Arch. Mus. Nac. Rio de Janeiro, vol. 7, p. 136, pl. 13, figs. 7, 8 (Maria Farinha, Pernambuco, Brazil).

1896 *Harpa* [*Pseudoliva*] *dechordata* White, Harris, Bull. Amer. Paleont., vol. 1, no. 4, p. 154.

Harpa bellardii var. *madachi* Noszky, 1940

Range—Oligocene of Hungary.

Remarks—This variety seems to me to have very little relationship with the Italian *Eocithara bellardii* Sacco, and probably represents a distinct species. However, the name is based on an internal mold with adhering remains of the shell, is described only very briefly, and from the illustration does not resemble any species in the Harpidae known to me. The ribs, very stout and few in number, do not appear to curve forward at the suture. Without a knowledge of the characters of

the aperture and ventral side of the shell it is impossible to discuss the affinities of this species, and even to be certain it is a member of this family.

Synonymy—

1940 *Harpa bellardii* var. *madachi* Noszky, Ann. Hist.-Nat. Mus. Hungarici. Min.-Geol.-Paleont., vol. 33, p. 34, pl. 2, fig. 11 (near Budapest, Hungary).

Eoharpa sinuosa Stephenson, 1955

Range—Upper Cretaceous of Mississippi and Missouri (Owl Creek formation).

Remarks—Proposed as a new genus in the family Harpidae, *Eoharpa* does not appear to belong in this family. The attenuation of the anterior end into a fairly long canal, the relatively high spire with fairly straight-sided whorls, and the presence of strong tubercles on the parietal and columellar callus are characters not found in any fossil or recent members in the family.

Synonymy—

1955 *Eoharpa sinuosa* Stephenson, U. S. Geol. Survey Prof. Paper 274-E, pp. 131-132, p. 23, figs. 3-6.

Harpa? *soriensis* Eames, 1952

Range—Eocene of Pakistan

Remarks—From the illustration and description I doubt very much that this species belongs in the Harpidae. It might be assigned to the Buccinidae s. lat.

Synonymy—

1952 *Harpa?* *soriensis* Eames, Phil. Trans. Royal Soc. London, Series B, no. 631, vol. 236, p. 106, pl. 4, fig. 91 (Zinda Pir section, Kohat District, Pakistan).

Harpa trimmeri Fleming, 1828

Range—Lower Eocene of London, England.

Remarks—According to information kindly furnished me by C. P. Nuttall and J. Cooper of the British Museum (Natural History), this species is very probably the volutid *Athleta tricornata* (J. Sowerby, 1840) from the London Clay, Lower Eocene.

Synonymy—

1828 *Harpa trimmeri* Fleming, History of British Animals, p. 342 (probably London Clay at Brentford).

Harpa neozelanica Suter, 1917

Range—Middle Eocene (Bortonian) of New Zealand (Waihao).

Remarks—Marwick (1934) suggests that Suter's type represents a gerontic specimen of what Su-

ter in the same paper described as *Tudicla neozelanica*. The latter species Marwick placed in his new genus *Fascioplex* (op. cit. p. 15) in the Fasciolaridae.

Synonymy—

- 1917 *Harpa (Ecithara) neozelanica* Suter, New Zealand Geol. Survey, Palaeont. Bulletin No. 5, p. 43, pl. 5, fig. 11 (Waihao River, South Canterbury, New Zealand).
 1934 *Fascioplex neozelanica* (Suter), Marwick, Proc. Malac. Soc. London, vol. 21, p. 16, pl. 1, fig. 8 (*Harpa (Ecithara) neozelanica* Suter listed as synonym).
 1966 *Fascioplex neozelanicus* (Suter), Fleming, New Zealand Dept. Sci. and Industr. Res., Bull. 173, p. 316, pl. 109, fig. 1341. (*Harpa neozelanica* Suter listed as synonym in explanation of plate).

Institutional Abbreviations

The following abbreviations for institutions are used in this paper:

- AMN—American Museum of Natural History, New York.
 AMS—Australian Museum, Sydney.
 ANSP—Academy of Natural Sciences, Philadelphia.
 AUCK—Auckland Institute and Museum, New Zealand.
 BM—British Museum (Natural History), London.
 BPBM—Bernice P. Bishop Museum, Honolulu.
 CAS—California Academy of Sciences, San Francisco.
 DMNH—Delaware Museum of Natural History, Greenville.
 MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts.
 MHNG—Museum d'Histoire Naturelle, Geneva.
 MNHP—Museum National d'Histoire Naturelle, Paris.
 NMV—National Museum of Victoria, Melbourne.
 RNHL—Rijksmuseum van Natuurlijke Historie, Leiden.
 SAM—South Australian Museum, Adelaide.
 TAU—Tel Aviv University, Tel Aviv.
 USGS—U. S. Geological Survey, Washington.
 USNM—National Museum of Natural History, Washington.
 WAM—Western Australian Museum, Perth.
 ZMC—Zoological Museum, Copenhagen.

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Key to the genera and subgenera of the family Harpidae

- A Protoconch multispiral (3 to 5 whorls), elevated-conical, whorls with a peripheral keel *Harpa*
- AA Protoconch paucispiral (2½ to 3 whorls), broadly conical or bulbous, whorls without peripheral keel B
- B Protoconch mamillate with planate apex, and 2½ to 3 convex whorls, suture impressed C
- BB Protoconch bulbous or dome-shaped, with 2 or fewer adpressed whorls D
- C Aperture length less than 60% of total length *Marwickara*
- CC Aperture length more than 70% of total length E
- D Protoconch bulbous, with large, inflated initial whorl *Austroharpa*
- DD Protoconch dome-shaped, with small initial whorl *Palamharpa*
- E Axial ribs widely separated, less than 18, parietal callus strong with marginate edge; protoconch small, rather turritid *Eocithara*
- EE Axial ribs crowded, more than 35; parietal callus thin, without sharp edge; protoconch large, broader than high *Refluharpa*

Plate 189, *Harpa* from the Eastern Pacific, Indo-Pacific and Eastern Atlantic

(*Opposite page*)

Figs. 1, 2. *Harpa crenata* Swainson, 1822. 1, Mazatlan, Sonora, Mexico (ANSP 250671); 2, Mulege Bay, Baja California, Mexico (USNM 12509).

Figs. 3-5. *Harpa gracilis* Broderip and Sowerby, 1829. 3, Vahitahi, Tuamotu Ids. (USNM 613243); 4, Baroia, Tuamotu Ids. (USNM 698318); 5, Papeete, Tahiti (Del. Mus. Nat. Hist. 12830).

Figs. 6-8. *Harpa amouretta* Röding, 1798, typical form. 6, 7 Siasi, Sulu Archipelago, Philippines (Del. Mus. Nat. Hist. 5185); 8, Ryukyu Ids. (USNM 670470).

Figs. 9-11. *Harpa amouretta* Röding, 1798, forma *crassa* Krauss, 1848. 9, Zanzibar (USNM 597117); 10, Cebu Id., Philippines (Del. Mus. Nat. Hist. 12528). 11, Mogadiscio, Somalia (USNM 673893).

Figs. 12-14. *Harpa doris* Röding, 1798. 12 and 13, Senegal (ANSP 180950); 14, Cape Verde Islands (Del. Mus. Nat. Hist. 122249).

Figs. 15, 16. *Harpa doris* Röding, 1798. Broad, heavy form. Ascension Island, South Atlantic. 15, (MCZ 278591); 16, (MCZ 232221).



Plate 189, *Harpa* from the Eastern Pacific,
Indo-Pacific and Eastern Atlantic
(explanation on opposite page)

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Family Harpidae Bronn, 1849

Genus Eocithara Fischer, 1883

This extinct genus comprises a group of species known only from the Lower Eocene to the Upper Miocene. They are all small, reaching a maximum length of 39 mm. (about 1½ inches), and have a paucispiral protoconch that is bluntly mammillate to broadly conical, with convex whorls and impressed sutures. The axial ribs or varices may be few (about twelve) or numerous and crowded and may be lamellar and sometimes slightly reflected or ridgelike and triangular in cross-section; the ribs at the shoulder are without spines, angular, or occasionally weakly spinose.

The genus *Eocithara sensu lato* comprises three subgenera: *Eocithara, sensu stricto*, *Marwickara* Laws, 1935 and *Refluharpa* Iredale, 1931. These subgenera have been summarily differentiated in the key given above.

The basic character differentiating *Eocithara* from the other genera of Harpidae is the paucispiral protoconch with a planate apex, and with the nuclear whorls without a peripheral keel but with impressed sutures. From *Harpa* it differs also in the generally much smaller size of its species, in the forwardly expanded upper part of the successive outer lips of the body whorl not fusing and covering most of the preceding whorl, and in the outer edge of the parietal callus being distinctly marginate. The genus *Austroharpa* differs in possessing a paucispiral, bulbous or dome-shaped protoconch, and in the forward curving upper part of the varices not prominent, or only slightly visible at the suture.

Subgenus Eocithara Fischer, 1883

Type: *Harpa mutica* Lamarck, 1803

The members of the typical subgenus are marked by their rather broadly ovate shape, short conical spire, well-developed parietal callus that is margined at its outer edge often leaving exposed a pseudumbilical chink at the siphonal fasciole.

The ten described species and subspecies assigned to *Eocithara s.s.* occur in deposits of

Lower Eocene to Lower Miocene age from California and Mississippi through France and Northern Italy to Burma, Java, and Fiji. A fragment apparently assignable to this subgenus was found in deposits of Upper Miocene age in the Marshall Islands.

Synonymy—

1881 *Harpa* Lamarck, Jousseume, Bull. Soc. Zool. France, vol. 5: Proc.-Verb., p. XXXVIII. Not *Harpa* Lamarck 1799, nor *Harpa* Röding, 1798.

1883 *Eocithara* Fischer, Man. de Conch., p. 601 (type by monotypy: *Harpa mutica* Lamarck.)

Eocithara morgani (Cossmann and Pissaro, 1909)

(Pl. 191)

Range—Upper Paleocene of Pakistan (Upper Ranikot).

Remarks—This, the earliest known species unquestionably assigned to the family, is undoubtedly closely related to *E. mutica* Lamarck from the Middle Eocene of France, in the ancestral line of which *E. morgani* may be considered to stand. A copy of the original description follows:

"Size moderate, shape depressed; spire conical, terminated by a smooth papillate protoconch of one whorl and a half; seven spire whorls, convex, depressed, separated by deep sutures, ornamented with thin, lamellar, distant ribs, slightly spinose posteriorly, regularly coinciding in successive whorls, decussated on the earlier whorls

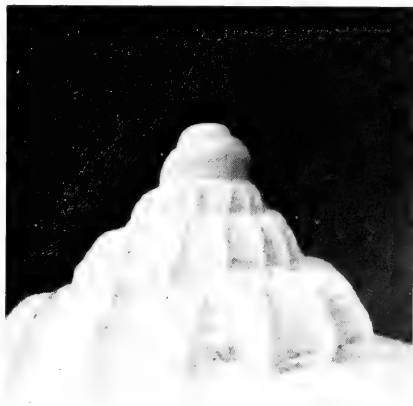


Plate 190. *Eocithara mutica* (Lamarck). Protoconch of specimen from Chaussy, France; Middle Eocene. USNM 646907. X 10.

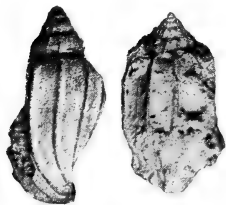


Plate 191. *Eocithara morgani* (Cossmann & Pissaro, 1909). Lower Eocene of Pakistan. Left-hand figure 33.9 mm. in length; right-hand figure 19.6 mm. (from Cossmann & Pissaro, 1909, pl. 2, fig. 25; pl. 3, fig. 24).

only, by a few spiral threads which are so thin as to be scarcely visible. Body-whorl very large, constituting almost the entire shell, excavated at its base. The axial lamellae persist upon the body-whorl up to its anterior region, while two or three axial threads, very thin, and of very slight relief, are intercalated amongst them, without spiral striations. It is only towards the base, in the excavated portion neighbouring the neck, that one distinguished some very fine spiral threads."

A plaster cast of the holotype, forwarded to me by M. V. A. Sastry of the Geological Survey of India, measures 33.9 mm. in length and 19.0 mm. in width.

The type locality is given by Cossmann and Pissaro as north of Leilan coal pit, Sind, Pakistan, from the upper beds of zone 3. Vredenburg (1928, p. 35) states that this is erroneous, and

that the two syntypes are from the uppermost beds (zone 4) of the Ranikot at Jhirak, Sind.

Vredenburg (1928, pp. 33-35) gives a more extensive and detailed description of this species.

Synonymy—

- 1909 *Harpa morgani* Cossmann and Pissaro, Mem. Geol. Survey India, Paleontologia Indica, n. s., vol. 3, mem. 1, p. 22, pl. 2, fig. 25, pl. 3, fig. 24.
1923 *Harpa (Eocithara) morgani* Cossmann and Pissaro, Vredenburg, Rec. Geol. Survey India, Paleontologia Indica, vol. 10, mem. 4, pp. 33-35 (Jhirak, Sind, Pakistan, Upper Ranikot).

Eocithara mutica (Lamarck, 1803)

(Pl. 192)

Range—Middle Eocene of France (Lutetian of Paris Basin).

Remarks—The type-species of *Eocithara* is a rather distinctive shell, and although not common in collections is the best known of all fossil species of the family Harpidae. The following description is based on five specimens in the collections of the National Museum of Natural History.

The species that Deshayes depicts for *Harpa mutica* Lamarck (Deshayes, 1824, pl. 86, figs. 14, 15) represents his "Var. a" (Deshayes, idem, p. 642), which he describes as being larger, more inflated, and with more distant ribs. This is quite distinct from the typical *mutica* Lamarck, and may be the *E. raricostata* Risso discussed below.

Description—Adult shell rather small, 24 to 39 mm. (1 to 1½ inches) in length, ovate, with a conical spire. Protoconch of 2½ to 2¾ whorls, with flattened apex and impressed suture, the whorls convex and smooth. Postnuclear whorls of spire convex, with sharp, lamellar, rather widely separated axial ribs that curve forward in the upper third of their length; in the body whorl this forward-curved upper end of each rib is adnate to the suture but does not reach the succeeding rib. Between the axial ribs there are strong, somewhat distant, spiral striae, subequal in strength, and crossed by distant, axial growth lines; below the suture, on the subsutural ramp, the spiral lines are fewer and more distantly spaced. The body whorl is gently convex, occasionally showing a distinct angulation at the shoulder, in which cases the spiral sculpture on the subsutural ramp is obscure or absent; axial ribs 12 to 14 in number, lamellar, occasionally slightly reflected, especially near the aperture, at the shoulder sometimes noticeably angulate; in the intercostal spaces the distantly spaced growth wrinkles are prominent, crossing the strong spiral sculpture and giving the



Plate 192. *Eocithara mutica* (Lamarck, 1807) Middle Eocene, Chaussy, France. USNM 646907 29.7 mm.

surface a netted appearance; siphonal fasciole strong, crossed by the strongly lamellose anterior end of the axial ribs. Aperture narrowly ovate, outer lip gently curved, smooth, reflected; inner lip forming a narrow callus on the parietal and columellar areas, with a conspicuous, slightly thickened margin, that in its anterior half is rather erect, and leaves exposed the pseudumbilical chink.

Measurements (mm.).—

length	width	no. whorls	
29.7	18.0	6.5	Chaussy
39.0	29.0(?)		original description
39.0*	24.9*		Chaussy

*Measured from figure in Cossmann and Pissaro, 1913

Synonymy—

1803 *Harpa mutica* Lamarck, Ann. Mus. Hist. Nat. Paris, vol. 2, pt. 2, p. 167; 1805, Lamarck, Ann. Mus. Hist. Nat. Paris, vol. 6, p. 227, pl. 44, fig. 14; 1824, Deshayes, Descr. Coq. Foss. Env. Paris, vol. 2, p. 642 [not pl. 86, figs. 14, 15 which represent Deshayes' var. a]; (Grignon, France).

1883 *Harpa (Eocithara) mutica* Lamarck, Fischer, Manuel Conch., p. 601; 1899, Cossmann, Essais Paléoconch. Comp., pt. 3, pp. 73, 75, fig. 10, pl. 3, figs. 22, 23; 1913, Cossmann and Pissaro, Icon. Compl. Coq. Foss. Eocene Paris, vol. 2, pl. 46, figs. 209-1.

***Eocithara mutica altavillensis* (Defrance, 1821)**

Range—Middle Eocene of France (Calcaire Grossier of western France).

Remarks—This form, described as a species by Defrance, has been declared to be merely a variety of *Eocithara mutica* (Lamarck) that is smooth between the ribs (Deshayes, 1865, p. 524). Without

seeing a specimen or figure, or even a description of this form I am unable to determine whether it should be ranked as a subspecies or a distinct species; for the present, therefore I am leaving it as a subspecies.

Synonymy—

- 1821 *Harpa altavillensis* Defrance, Dict. Sciences Naturelles, vol. 20, p. 303 (Hauteville, Dept. de la Manche).
1865 *Harpa mutica* var. *altavillensis* Defrance, Deshayes, Descr. Anim. sans Vert Bassin de Paris, vol. 3, p. 524.

***Eocithara mutica californiensis* (Vokes, 1937)**

(Pl. 193)

Range—Middle Eocene of California (Domenige stage).

Remarks—Vokes is undoubtedly correct in considering this a subspecies of the *Harpa mutica* Lamarck from the Calcaire Grossier of France. The differences mentioned by Vokes are slight—one less axial rib on the body whorl and the presence of spiral sculpture on the subsutural ramp.

Description (copied from Vokes, 1937)—Types: Holotype, Univ. California Mus. Paleont. 30438; paratypes, U.C.M.P. 30439, 30440; loc. 3296, Lajas formation, Aliso Canyon, Ventura County, California.

Dimensions: Holotype, length 26.4 mm., diameter (crushed), 16.2 mm.; paratype 30439, length, 19.8 mm., diameter (crushed), 9.7 mm.; paratype 30440, length (incomplete), 18.2 mm., diameter, 11.2 mm.

Shell of moderate size, subfusiform, globose; nucleus smooth, papillate, of approximately three whorls; post-nuclear whorls five, convex, shouldered, with somewhat appressed sutures, ornamentation consisting of prominent, distant, lamellar axial ribs decreasing in number from 15 to 17 on the first post-nuclear whorl to 10 to 12 on the body whorl; interspaces ornamented with numerous (6 to 15), secondary axial riblets; spiral sculpture of numerous, irregularly spaced primary and secondary riblets, the secondary ribbing tending to extend up on the shoulder of the whorl; aperture more than twice the length of the spire, moderately narrow; outer lip simple, inner lip with a well-developed characteristic callus wash, anterior canal short; base of shell concave, with a well-developed fasciole.

Synonymy—

- 1936 *Harpa (Eocithara) mutica* n. subsp. Vokes mss., Bull. Geol. Soc. America, vol. 47, p. 871 [nomen nudum].
1937 *Harpa (Eocithara) mutica californiensis* Vokes, Jour. Paleont., vol. 11, p. 11, pl. 2, figs. 2, 4, 6, 8.



Plate 193. *Eocithara mutica californiensis* (Vokes, 1937). Middle Eocene of California. 26.4 mm. (from Vokes, 1937, pl. 2, figs. 2, 6).

***Eocithara mutica hilarionis*
(Gregorio, 1880)**

(Pl. 194)

Range—Middle Eocene of Northern Italy (Upper Lutetian).

Remarks—This subspecies is very close to the nominal species, and its validity as a distinct taxon is somewhat doubtful. The principal differences according to the author are the smaller number of ribs—10 or 11 rather than the 12 to 14 found in *mutica* s. str.—and stronger cancellate sculpture between the ribs.

Because Gregorio's work is rare and unavailable to most students, I give a free translation of the original diagnosis:

"It is rather common at San Giovanni, although complete specimens are rarely found. It reaches there a fair size: the figured specimen has a length of 35 mm., a width of 23 mm., and a spire angle of 83°; another specimen is almost 33 mm. long. Some characters are present that are different from the form found in the Paris Basin, not enough to make it a distinct species, but sufficient to consider it a well-defined variety. The principal differences are the following: the form is much more oblong than the figure given by the worthy Deshayes [this is *H. mutica* var. a Deshayes, possibly the same as *E. raricostata* (Risso, 1826)], but more like that given by Lamarck (p. 40, pl. 44. Mem. sur les foss. des environs de Paris); ribs of the body whorl usually ten or eleven; between them an elegant, net-like, cancellate sculpture, which is formed by numerous spiral threads and fewer (about 5), more prominent axial ones that resemble sometimes little riblets. Neither Deshayes nor Lamarck note this difference, but the figure of the latter author distinctly shows the axials while the spirals are lacking; evidence of the supremacy of the former over the latter. The number of whorls is six or seven; the first smooth,

submamillate; the last whorl large, but not as globose as that figured in the work of Deshayes in which the posterior convexity seems to cover part of the spire. This species seems to have been found at Croce Grande by Bayan, and listed in his Catalogue as *Harpa* cf. *mutica* Lamarck."

Synonymy—

1880 *Harpa mutica* var. *Hilarionis* Gregorio, Fauna di S. Giovanni Ilarione (Parisiano). Parte I. Cefalopodi e Gastropodi, p. 42, pl. 5, figs. 43a, b.

***Eocithara clarki* (Vokes, 1937)**

(Pl. 195)

Range—Middle Eocene of California (Domengine state).

Remarks—This species is more narrow than any other known species of *Eocithara*, with a higher spire, and without any secondary spiral sculpture.

Description (copied from Vokes, 1937)—Holotype: Univ. California Mus. Paleont. 15792; loc. A-1165, Big Tar Canyon, south of Coalinga, California; Domengine formation.

Dimensions: Length, 26.4 mm.; diameter, 14.6 mm.

Shell of moderate size, thin, subfusiform; spire high, of five post-nuclear whorls, ornamented with slightly sinuous, lamellar axial ribs separated by broad interspaces marked by five narrow, secondary axial threads and numerous spiral ribs of equal strength, separated by interspaces about twice the width of the spiral; with 13 axial lamellae on the third post-nuclear whorl, 14 on the penultimate, and 16 on the ultimate whorl; whorls shouldered but slightly, sutured appressed, distinct; aperture twice the length of the spire, nar-



Plate 194. *Eocithara mutica hilarionis* Gregorio, 1880. Middle Eocene of Italy. Holotype. 35 mm. in length (from Gregorio, 1880, pl. 5, figs. 43a, b).



Plate 195. *Eocithara clarki* (Vokes, 1937). Middle Eocene of California. 26.4 mm. (from Vokes, 1937, pl. 2, figs. 5, 7).

row; outer lip simple, inner lip with a characteristic callus wash; base of the shell concave, recurved to a strong fasciole ornamented with the axial lamellae.

Synonymy—

1937 *Harpa (Eocithara) clarki* Vokes, Jour. Paleont., vol. 11, p. 11, pl. 2, figs. 5, 7.

Eocithara raricostata (Risso, 1826)

Range—Upper or Middle Eocene of southern France (Alpes Maritimes).

Remarks—This species, very briefly described and unfigured, has been ignored by all later workers. Judging from the short diagnosis, it is characterized by its broad inflated shape and distant axial ribs. It may be that this is the same as the *Harpa mutica* var. *a* of Deshayes (1824, Descr. Coq. Foss. Env. Paris, vol. 2, p. 642, pl. 86, figs. 14, 15) which has the same characteristics, and was found at Parnes in the Paris Basin. Only an examination of the type, if it exists, can determine its relationship with the other known Eocene species.

Synonymy—

1826 *Harpa raricostata* Risso, Hist. Nat. Europe Merid., vol. 4, p. 180 ("Calcaire grossier de nos montagnes").

Eocithara elegans (Deshayes, 1835)

(Pl. 196)

Range—Upper Eocene of France (Auversian of Paris and Nantes Basins).

Remarks—This species is somewhat less inflated than *E. mutica* (Lam.), and is described as possessing a sharper subsutural angle on the body whorl. The figures, however, given by Cossmann and Pissarro (1913, pl. 46, figs. 209-2) show a shell

with a rather rounded subsutural shoulder. The spiral sculpture is stronger than in *E. mutica*. *E. elegans* shows some relationship with *E. submutica* Orb.

Description (freely translated from original diagnosis)—This *Harpa* is ovate-oblong, a little more cylindrical than the preceding species [*H. mutica* Lam.]; its spire is short: with six very narrow [= low] whorls of which the last are flattened above. There are thirteen or fourteen longitudinal ribs on the last whorl; these ribs are thicker than in the preceding species, and they are elongated a little in their upper part, as in *Harpa nobilis*. The intervals between the ribs show rather strong distant, unequal transverse striae, a finer one being situated between the stronger ones. These striae form an elegant network with other regular and much finer longitudinal ones. The aperture is proportionately larger than in the other species; the left border is much more narrow, especially at the base of the columella where it leaves uncovered the oblique and scaly fasciole which ends at the terminal notch of the aperture.

The largest specimen that we know of this rare and precious species is 33 mm. long and 20 mm. wide.

Synonymy—

1835 *Harpa elegans* Deshayes, Descr. Coq. Foss. Env. Paris, vol. 2, p. 643, pl. 86, figs. 16-18; 1844, Deshayes, Hist. Nat. An. s. Vert., Ed. 2, vol. 10, p. 134 (Valmoulois, France).

1913 *Harpa (Eocithara) elegans*, Cossmann and Pissarro, Icon. Compl. Coq. Foss. Eocene Env. Paris, vol. 2, pl. 46, fig. 209-2.

Eocithara jacksonensis (Harris, 1896)

(Pl. 197)

Range—Upper Eocene of Mississippi (Jackson formation).

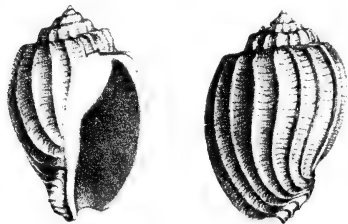


Plate 196. *Eocithara elegans* (Deshayes, 1835). Upper Eocene of France. X 1. (from Deshayes, 1835, pl. 86, figs. 16, 17.

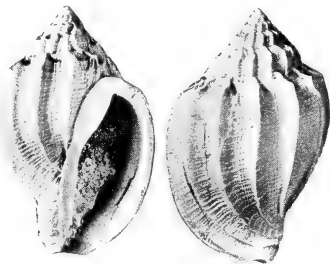


Plate 197. *Eocithara jacksonensis* (Harris, 1896). Upper Eocene of Mississippi. 29.5 mm. (from Harris and Palmer, 1947, pl. 56, figs. 19, 20).

Remarks—This species is a typical member of the genus *Eocithara*. The ribs are fewer in number and heavier than in *E. mutica* (Lamarck), with the intercostal sculpture more pronounced. I have seen two rather poor specimens of this species in the collection of the National Museum of Natural History, of which one measures 31 mm. in length and 18 mm. in width. The holotype measures: length, 31.5 mm.; width 18.7 mm.

Description (copied from Harris, 1896)—“Size and general form as indicated by the figure; volutions 8; 1 and 2 very minute, smooth; 3 much larger, smooth; 4 somewhat larger than 3, showing vertical costae in its first half, then assuming the characteristic markings of the remaining whorls; costae on the body-whorl nine in number, somewhat deflected below the suture as in *Drillia*; between the costae the shell is finely cancellated with a network of raised lines; anterior canal slightly larger than usual for the genus. Locality, Jackson, Miss.”

Synonymy—

1896 *Harpa jacksonensis* Harris, Proc. Acad. Nat. Sci. Philadelphia, vol. 48, p. 472, pl. 18, fig. 10.

1947 *Harpa (Eocithara) jacksonensis* Harris, Harris and Palmer, Bull. American Paleont., vol. 30, no. 117, p. 397, pl. 56, figs. 19, 20.

Eocithara birmanica (Vredenburg, 1923)

(Pl. 198)

Range—Upper Eocene of Burma (Yaw stage).

Remarks—This species, very briefly described by the author, is based on an incomplete specimen. A plaster cast of the holotype, kindly sent to the National Museum of Natural History by M. V. A. Sastry of the Geological Survey of India, measures 19.1 mm. in length and 12.0 mm. in width. The type was collected at Thetkeygin, Burma.



Plate 198. *Eocithara birmanica* (Vredenburg, 1923). Upper Eocene of Burma. 19.1 mm. left-hand figure, plastercast of holotype; right-hand figure from Vredenburg, 1923, pl. 14, fig. 6.

Description (copied from Vredenburg, 1923)—“Although the solitary available specimen is very incomplete, its distinct characteristics make it worthy of record. It is very closely related to *Harpa mutica* Lamk. of the Middle Eocene of the Paris region, from which it is distinguished by its smaller size and the much more delicate intercostal reticulation. The latter character distinguishes it still more decidedly from *Harpa Morgani* C. and P. occurring in the Lower Eocene of Sind. Compared with *Harpa narica* Vred. from the Oligocene of Sind, the Burmese shell is smaller, with a relatively taller spire and with wider-spaced axial lamellae.”

Synonymy—

1923 *Harpa (Eocithara) birmanica* Vredenburg, Rec. Geol. Survey India, vol. 54, p. 252, pl. 14, fig. 6 (Thetkeygin, Burma).

Eocithara submutica (Orbigny, 1852)

(Pl. 199)

Range—Lower Oligocene of southern France (Dax, Landes).

Remarks—I have been unable to find a description of this species which is based on a name accompanying a pair of figures. These original figures show a great resemblance to the figures for *E. elegans* (Deshayes) from the Upper Eocene of the Paris Basin. I have found no references to this species later than that by Cossmann (1899, p. 76) who assigns it to the Tongrian (lowest Oligocene of Upper Eocene); some later workers place the beds whence this species is supposed to come in the Stampian, or Middle Oligocene.

Synonymy—

1845 *Harpa mutica* Lamarck, Grateloup, Conch. Foss. Tert. Bassin Adour, vol. 1, Atlas, 1840-1845, suppl. pl. 1, figs. 21, 22 (Dax, Landes, France).

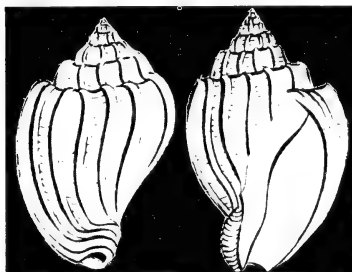


Plate 199. *Eocithara submutica* (Orbigny, 1852). Lower Oligocene of France. X 2. (from Grateloup, 1845, pl. 1, figs. 21, 22).

1852 *Harpa submutica* Orbigny, Prodr. Paléont., vol. 3, p. 17.
New name for *H. mutica* Grat., 1845, not Lamarck, 1803.

1899 *Harpa (Eocithara) submutica* Orbigny, Cossmann, Essais Paléoconch. Comp., pt. 3, p. 76.

Eocithara narica (Vredenburg, 1925)

(Pl. 200)

Range—Oligocene of Pakistan (Nari formation).

Remarks—The figures given by Vredenburg are poor, but I have been able to examine plaster casts of the syntypes of this species. These together with his lengthy description suggest that *narica* has some resemblance to certain species of *Harpa*, especially in the ovate shape of the body whorl without a shoulder angulation, and in the apparent junction of the forward curving upper ends of the successive axial ribs. Indeed, Vredenburg suggests that this species may represent an ancestral form of *Harpa conoidalis* (= *major* Röding). Nevertheless, I am retaining this species in *Eocithara* because of the restricted and marginate parietal and columellar callus, the uncertainty over the nature of the protoconch, and because of the age of the beds in which the species is found.

Description (abbreviated from the original description)—The elongate-ovoid shell has a low, broadly conical spire, the body whorl measuring nine-tenths of the total length. The small eroded protoconch is followed by three and a half convex whorls, the sutures of which are covered by the junction of the forward curving upper ends of the successive axial ribs. These number from 15 to 16 on the spire whorls, and from 14 to 15 on the body whorl, and show a slight spinosity at the rounded shoulder of the whorls. Between the ribs is a delicate network of fine axial and spiral threads. The parietal callus is conspicuously margined by a

low, raised edge, and the rectilinear edge of the columellar callus is slightly raised at the pseudumbilical chink on the inner side of the siphonal fasciole.

Measurements (in mm.)—

Height	29.3	41.0
Diameter	17.0	24.0
Height of spire	5.4	6.5
Height of body whorl	26.5	35.0

Synonymy—

1925 *Harpa (Eocithara) narica* Vredenburg, Mem. Geol. Survey India, vol. 50, p. 122, pl. 1, fig. 16, pl. 2, fig. 6 (Bhagothoro Hill, Sind, Pakistan).

Eocithara bellardii (Sacco, 1890)

(Pl. 201)

Range—Oligocene of northern Italy.

Remarks—Although the brief diagnosis (copied in free translation below) does not mention any characters that assist us in determining whether this species is an *Eocithara* or a *Harpa*, the illustration given by Sacco does show the narrow parietal and columellar callus, the strongly angulate body whorl, and ribs that are apparently not strongly curved forward at the sutural margin. For these reasons I am placing the species in the genus *Eocithara*.

Description (from Sacco, 1890)—Shell of medium size, oblong ovate. Spire fairly high. Whorls about six, with heavy, somewhat rounded, very elevated longitudinal ribs; 12-13 subarcuate ribs in last whorl, which generally alternate with the ribs of the penultimate whorl. Surface between the ribs sculptured with numerous very fine transverse striae. Aperture subfusiform. Outer lip slightly thickened. Columella subumbilicate. Siphon somewhat elongate. Height 30 mm., width 18 mm.

Synonymy—

1890 *Harpa bellardii* Sacco, Moll. Terr. Terz. Piemonte Liguria, pt. 7, p. 9, pl. 1, figs. 1a, 1b (Tongrian of Cassinelle, Dego, Monfese).



Plate 200. *Eocithara narica* (Vredenburg, 1925) Oligocene of Pakistan. 29.0 mm. Plastocast of syntype, USNM.

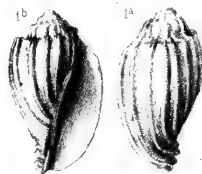


Plate 201. *Eocithara bellardii* (Sacco, 1890). Oligocene of northern Italy. 30 mm. (from Sacco, 1890, pl. 1, figs. 1a, 1b).

***Eocithara muticaeformis* (Martin, 1916)**

(Pl. 202)

Range—Lower Miocene of Java (Gunung Spolong, West Progo Mountains).

Remarks—This species appears to be the latest representative of *Eocithara*, with which it agrees, as Martin points out, in the nature of the parietal callus, the umbilical chink, and the character of the junction of the ribs at the suture. It is beginning to show some relationship with species of *Harpa* in that the outer edge of the parietal callus is thin and is not sharply margined at the outer edge.

Description (freely translated from original)—Shell ovate, somewhat inflated, anteriorly attenuate. The protoconch button-shaped, consisting of two small smooth whorls, the intermediate whorls strongly convex, with high, narrow, axially oriented, slightly curved ribs which in the early whorls develop a bluntly angulate point near the suture. That makes it appear as if a spirally oriented angulation, actually absent, were present [on the body whorl]. Between the distant ribs the surface is covered with fine spiral ridges; they are also separated and number up to six.

The body whorl has fourteen ribs which are curved forward at the suture which they almost cover; a spiral sculpture similar to that on the spire whorls, is present only on the sutural ramp.

The columella is slightly concave in the middle; the inner lip very thin but bordered in its anterior half by a definite furrow, and with the margin distinctly erect over the weakly indicated umbilical chink. The latter is surrounded by a strong spiral fasciole conforming to the siphonal canal, and over which the axial ribs continue in undiminished strength in a sickle-like curve. The outer lip is missing. Length 20 mm.

***Synonymy*—**

1916 *Harpa* (*Eocithara*) *muticaeformis* Martin, Samml. Geol. Reichs-Museums Leiden, N.F., vol. 2, pt. 6, p. 231, pl. 1, figs. 15, 15a (Gunung Spolong, West Progo Mts., Java).



Plate 202. *Eocithara muticaeformis* (Martin, 1916). Lower Miocene of Java. 20 mm. (from Martin, 1916, pl. 1, figs. 15, 15a).

Eocithara species

(Pl. 203)

Range—Lower Eocene (Mangaorapan stage) of New Zealand.

Remarks—This specimen is of interest as it represents the second oldest known species of the Harpidae, and also because it shows the wide range that *Eocithara* had in Lower and Middle Eocene times, throughout the extent of the Tethys Sea, from California, across Europe and India, to New Zealand.

Although new species have been described from poorer specimens than this one, it is inadvisable to give this single specimen a name. I am merely putting it on record to fill out the distributional picture of the genus. The figures adequately show that the characters of the shape of shell and of the ribs appear to be those of a typical *Eocithara*. Shell length 27.9 mm., width 15.2 mm.

Locality—Tuffs in bed of Whit's Creek, Eyre River District, Canterbury, New Zealand. Collected by J. Gellen, January, 1960.

Age—Mangaorapan stage—equivalent of about upper Ypresian stage; Lower Eocene.

The above information and the photographs were kindly sent me by Dr. Alan Beu of the New Zealand Geological Survey.

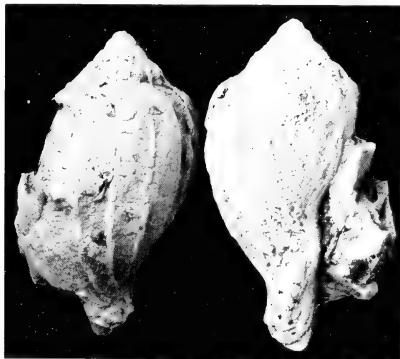


Plate 203. *Eocithara* species. White's Creek, Eyre River District, Canterbury, New Zealand. Lower Eocene (Mangaorapan stage). New Zealand Geological Survey.

Eocithara species

(Pl. 204)

Range—Middle Eocene of Texas (Claiborne formation of easternmost Texas).

Remarks—The fragmentary specimen is presented here to indicate the presence of a species of



Plate 204. *Eocithara* sp. Middle Eocene of Texas. 14 mm. (from Palmer, 1937, pl. 65, fig. 6).

Eocithara in the Middle Eocene of North America. It has wider ribs and somewhat weaker intercostal sculpture than does *E. jacksonensis* (Harris) from the Jackson formation of the Upper Eocene.

The locality is in eastern Sabine Co., Texas, on the edge of the Sabine River, east of Hemphill.

Synonymy—

1937 *Harpa* sp. Palmer, Bull. American Paleontology, vol. 7, no. 32, p. 398, pl. 65, fig. 6 (eastern Sabine Co., Texas).

Eocithara species

Range—Upper Miocene of Eniwetok, Marshall Islands.

Remarks—A fragment 15 mm. long from a drill-hole (No. E-1) on Parry Island, Eniwetok, Marshall Islands, is referred with some doubt to this genus. Only the anterior canal and sinus, the lower portion of the columellar lip, and a part of the body whorl comprising three complete ribs from their procurved upper end to the siphonal fasciole and anterior canal is present.

My assignation of this fragment to *Eocithara* is based on the low, not broadly expanded, procurved end of the ribs, and the nature of the siphonal fasciole—strongly convex on the ventral surface and separated from the lower end of the columellar callus by a deep furrow which suggests a pseud-umbilical chink.

The fairly crowded ribs are low, somewhat flattened in their upper portion, with faint, paired color lines visible under magnification. The inter-spaces show flattened spiral cords crossed by irregular axial growth striae. The crowded microscopic axial striae present in *Harpa major* Röding are absent, and the aspect of the sculpture is generally distinct from that found in the recent species of *Harpa*.

This fragment was found in the portion of a drillhole recovered from 830-840 feet, and is assigned by Ladd (1966, p. 7) to the Upper Miocene.

Further, more complete material is needed to prove the generic allocation. If this placement is correct it is the latest known occurrence for *Eocithara*.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Eocithara waihaoensis Laws, 1935

(Pl. 205)

Range—Middle Eocene of New Zealand.

Remarks—The following description is based on the holotype and two fragments kindly sent me on loan by Mr. Walter O. Cernohorsky of the Auckland (New Zealand) Institute and Museum.

Description—Shell relatively small (23 mm. in length), ovate, with rather high spire (more than one third of total length, as compared with less than one fourth of total length in *Eocithara*). Protoconch somewhat worn but showing rather flattened nuclear whorls. Early post-nuclear whorls also somewhat worn, with fairly strong opisthocline ribs; maximum curvature at shoulder of whorls; ribs numbering twenty in number in penultimate whorl, bluntly angulate in cross-section, not lamellar, with interspaces marked by strong, subequal spiral cords crossed by irregular growth wrinkles; the anterior ends of the ribs form only low ridges on the weakly differentiated siphonal fasciole. Aperture rather narrow, outer lip thickened internally, somewhat reflected, sinuous in profile with a shallow posterior sinus and prosocyrty medially. Inner lip with a distinct and slightly thickened outer margin, which in the type is broken. Siphonal canal moderately long, directed to the left.

Specimens examined—*Holotype* (Auckland Inst. and Museum): length, 23 mm., width 12.3 mm.; greensands, Waihao Downs, South Canterbury, New Zealand (Bortonian, Middle Eocene). Paratypes: two fragments from same collection.

Synonymy—

1935 *Eocithara* (*Marwickara*) *waihaoensis* Laws, Trans. Royal Soc. New Zealand, vol. 65, p. 29, fig. 11 (Waihao Downs, South Canterbury, New Zealand).

Subgenus Marwickara Laws, 1935

Type: *Eocithara* (*Marwickara*) *waihaoensis* Laws, 1935

This subgenus was proposed by Laws for a single species from the Middle Eocene of New Zealand. It had been sent to Dr. J. Marwick for examination whose summary of the differences between the New Zealand species and the type species of *Eocithara* are quoted by Laws.

The principal differences distinguishing this subgenus are the more narrowly ovate shape and higher spire, a protoconch with more flattened, less convex whorls, and a neck and anterior canal that is somewhat twisted to the left. The parietal "denticle" seen on the parietal wall about a third of the distance down from the posterior angle with the outer lip, with a lower obscure swelling below it, may be due merely to an irregularity covered over by the parietal wall.

Synonymy—

1935 *Marwickara* Laws, Trans. Royal Soc. New Zealand, vol. 65, p. 28 (Type by original designation: *Marwickara waihaoensis* Laws).



Plate 205. *Eocithara* (*Marwickara*) *waihaoensis* Laws, 1935. Holotype, Waihao Downs, South Canterbury, New Zealand;

Middle Eocene. 23 mm. Auckland Institute and Museum.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Subgenus *Refluharpa* Iredale, 1931

Type: *Harpa lamellifera* Tate, 1889

This subgenus contains only one species, *E. (Refluharpa) lamellifera* Tate from the Middle Miocene of Victoria. Iredale proposed the genus *Refluharpa* for this species, which Finlay in the same year had placed in *Eocithara*. Cotton and Woods (1933, pp. 45, 47) made *Refluharpa* a synonym of *Eocithara* because of the similarity of the protoconch.

However, the protoconch of *E. lamellifera* is considerably larger than that of *E. mutica* Lamarck; the maximum diameter of the protoconch of a specimen of the former being more than twice as great as that of an example of *E. mutica*; the number of whorls is generally greater $2\frac{1}{2}$ to 3 as opposed to $2\frac{1}{4}$ in *mutica*; the apex is more planate with the suture more deeply impressed; the parietal callus is not strongly marginate but is thin and evanescent near its outer edge.

These differences plus the later age of *E. lamellifera*, induce me to retain the species in a distinct subgenus.

Synonymy—

1931 *Refluharpa* Iredale, Rec. Austral. Museum, vol. 18, pp. 230, 233 (June 29).

Eocithara lamellifera (Tate, 1889)

(Pls. 206, 207)

Range—Middle Miocene (Balcombian-Bairnsdalian) of Victoria.

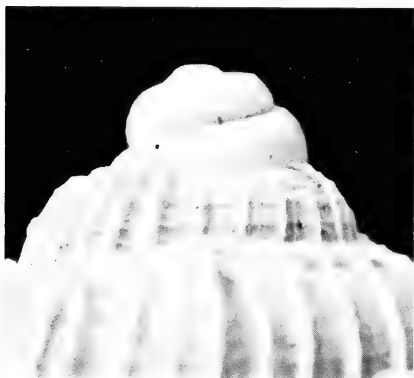


Plate 206. *Eocithara (Refluharpa) lamellifera* (Tate). Protoconch of specimen from Muddy Creek, Hamilton, Victoria; Middle Eocene. USNM 646909. X 10.

Remarks—In addition to the differences listed above under the subgenus, this species is marked by the great number of strongly lamellar ribs—more than 35 on the body whorl of a specimen 24.5 mm. in length, by the subsuturally planate whorls, the prominent spiral sculpture between the ribs which is particularly prominent in the penultimate whorl.

It is found in several localities in Victoria—Muddy Creek, Hamilton (the type locality); Balcombe Bay, Port Phillip Bay; near Altona, Port Phillip Bay; Shelford, near mouth of Gellibrand River.

Measurements (mm.)—

length	width	
32	21.5	Holotype (SAM-T-698)
36	22	Paratype (SAM-T-698)
24.5	16.1	USNM 646909
23.6	15.9	USNM

Synonymy—

1889 *Harpa lamellifera* Tate, Trans. Proc. Roy. Soc. South Australia, vol. 11, p. 149, pl. 6, fig. 2 (lower beds, Muddy Creek, Victoria).

1897 *Harpa (Eocithara) lamellifera* Tate, Harris, Cat. Tertiary Moll., Dept. Geol. British Museum, pt. 1, p. 79, pl. 4, fig. 3 a-b.

1931 *Eocithara lamellifera* Tate, Finlay, Trans. New Zealand Inst., vol. 62, pp. 12, 13 (May 31); 1933, Cotton and Woods, Records South Australian Museum, vol. 5, pp. 45, 47.

1931 *Refluharpa lamellifera* Tate, Iredale, Records Australian Museum, vol. 18, p. 230 (June 29).

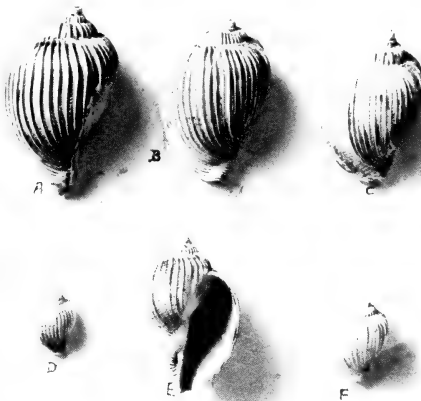


Plate 207. *Eocithara (Refluharpa) lamellifera* (Tate). Holotype (30.5 mm.) and paratypes. South Australian Museum, Tate Colln. 698.

[These occasional blank areas occur between genera and subgenera to permit the insertion of new material and future sections in their proper systematic sequence.]

Genus *Harpa* Röding, 1798

Type: *Harpa harpa* Linné, 1758

The genus *Harpa* comprises nine recent and five fossil species. Seven of the living species are found in the Indo-Pacific region and one each on the West African coast and in the eastern Pacific. The fossil species are found in beds of from Oligocene to Pliocene age.

The shells are characterized by their relatively large body whorl bearing a variable number of axial lamellar or sublamellar ribs, the rather extensive parietal and columellar callus which is not sharply marginate abaperturally, and by the whorls of the spire, especially the penultimate and antepenultimate whorls, being more or less covered by the glaze of the expanded posterior part of the axial ribs. The protoconch is elevated-conic, consisting of from 3 to 5 whorls, usually flesh-pink to purplish red, sometimes whitish in color, with a distinct keel at the periphery, just visible above the suture. The basic color pattern is a banded one, the axial ribs marked with alternating spots of various shades of pink and white, with or without dark horizontal lines, these spots coinciding on successive ribs; the banded effect thus created is strengthened by the irregular, axial, zigzag and festooned dark lines and white spots in the spaces between the ribs, this pattern also being repeated in the successive interspaces, with the adapertural projections of the festoons always coinciding with the white spaces on the axial ribs. In *Harpa costata* much of the color pattern is obscured by the dense axial sculpture. The anterior siphonal notch is rather broad and open, not narrow and somewhat constricted as in *Eocithara*.

Synonymy—

- 1798 *Harpa* Röding, Museum Boltenianum, p. 149 (type by tautonymy: *Harpa harpa* Linné).
 1799 *Harpa* Lamarck, Mem. Soc. Hist. Nat. Paris, vol. 1, p. 71 (type by tautonymy: *Harpa harpa* Linné).
 1806 *Harpalis* Link, Besch. Nat.-Sammlung Univ. Rostock, pt. 3, p. 114 (type here designated: *Harpa major* Lamarck).
 1815 *Harparia* Rafinesque, Analyse de la Nature, p. 145. New name for *Harpa* Lamarck, 1799.
 1934 *Lyra* Griffith and Pidgeon, Cuvier's Animal Kingdom, vol. 12, p. 234. *Nomen nudum*.
 1881 *Cithara* "Klein" Jousseaume, Bull. Soc. Zool. France, vol. 5: Proc.-Verb., p. xxxviii (type here designated: *Harpa harpa* Linné).

Nomenclature—Some authors have credited the name *Harpa* to Walch, 1771, or have cited an earlier usage of the name, namely *Harpa* Pallas, 1774. The first is based on Herrmannsen's citation (Herrmannsen, 1846-47, p. 501), who gives, however, an erroneous reference. On page 113 of volume 2, part 1 (not volume 3, p. 113), Walch discusses the "Harfenschncken" but without using a Latin name; furthermore, Walch's work is non-binominal.

Pallas in his "Spicilegium Zoologia" used *Harpa nobilis* as a vernacular group name in connection with his description of *Buccinum geversianum* (= *Trophon* g.). As such, in addition to being in the plural form, it is not available as a validly proposed taxon.

Harpa harpa (Linné, 1758)

(Pl. 187, figs. 7-10)

Range—From East Africa to Tonga.

Remarks—This species is characterized by its stout, broadly ovate, markedly shouldered shell, with three separated chestnut blotches on the ventral side, the ribs rather strong, flattened, and marked with many distinct lines arranged in groups; a band of interrupted and irregular blotches of orange brown or reddish brown is generally present about the middle of the body whorl.

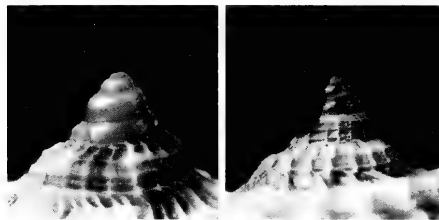


Plate 208. Enlarged protoconchs of species of *Harpa*. Fig. 1. *Harpa ventricosa* Lamarck. USNM 7421a. Fig. 2. *Harpa articularis* Lamarck. Off Tambizen, North Borneo, USNM 666808.

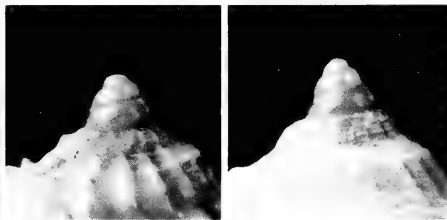


Fig. 2. *Harpa harpa* (Linné). USNM 7421. Fig. 4. *Harpa crenata* Swainson. Mulege Bay, Baja California, Mexico, USNM 12509. (all X 5).

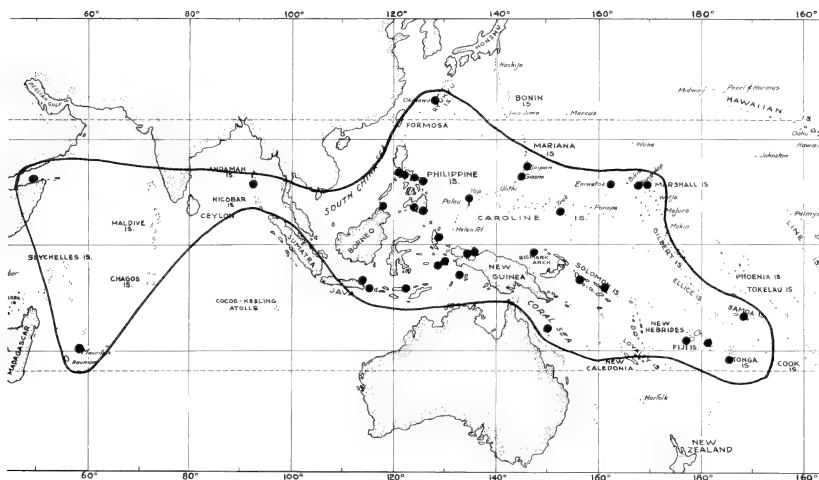


Plate 209. Geographical distribution of *Harpa harpa* (Linné).

The distribution of this species appears to be centered in the Philippines and Indonesia—Abbott's Western Pacific Arc—whence it has spread in to what I term eastern Melanesia, to the Samoan Islands and Tonga, and in the north into northern Micronesia. It is relatively scarce in the Indian Ocean.

Description—Adult shell 42 to 76 mm. (1½ to 3 inches) in length, rather solid, broadly ovate, with a low conical spire, and a last whorl that is bluntly angulate below the shoulder. Nuclear whorls (Pl. 208) 3 to 3½, rosy pink in color, convex, smooth; early postnuclear whorls flattened, smooth on top, made angulate by a spiral ridge at shoulder with one or two below that, and with low, distant, slightly curved axial ribs; the portion of the whorls below the shoulder becomes increasingly covered by the callus that is formed by the successive anterior extensions of the axial ribs that flatten out and cover the adjacent part of the preceding whorl, and finally spread to above the shoulder ridge and over the entire subsutural ramp. Body whorl with a flattened subsutural ramp, markedly though roundly angulate at the shoulder which is marked by strong spines on the ribs; ribs rather broad, crossed by many fine dark lines that are usually present in groups of three or four. Between the ribs the basic color is of various shades of pink and flesh color, marked by whitish pink spiral bands of varying width, the widest just below the shoulder and all with distant chestnut spots; in the

middle of the whorl is a band of irregularly squarish blotches of rust color or red brown that occur generally in every other interspace; the interspaces are marked also by wavy axial stripes of reddish brown. Aperture broadly ovate, rather patulous below, inner lip almost straight, outer lip gently arcuate, thickened within, and subdentaculate along basal half; the interior of outer lip conspicuously marked by dark chestnut at the terminations of the darker spiral bands. The thin glaze covering the ventral side is marked by three distinct reddish brown blotches—anterior, middle, and posterior.

Measurements (mm.)—

length	width	no. whorls	
75.7	50.3	6½	large; no data
71.5	46.9	6½	large; Okinawa, Ryukyus
65.8	43.8	6	average; Guam, Marianas
51.8	33.8	5½	small; Okinawa, Ryukyus

Synonymy—

- 1758 *Buccinum harpa* Linnaeus, *Systema Naturae*, ed. 10, p. 738, no. 400 (ad Benghalia). Refers to Pétiver, pl. 48, fig. 13; Rumphius, pl. 32, fig. 1; Gualtieri, pl. 29, fig. C. E; and others; 1956, Dodge, *Bull. Amer. Mus. Nat. Hist.*, vol. 111, art. 3, pp. 196-198.
- 1798 *Harpa nobilis* Röding, *Mus. Bolten.*, p. 150; refers to Martini, *Conch. Cab.*, vol. 3, p. 415, pl. 119, fig. 1091 (no locality); 1822, Lamarck, *Hist. Nat. Anim. s. Vert.*, vol. 7, p. 256 (*Océan des Grandes Indes*). 1835, Kiener, *Spec. Gen. Icon. Coq. Viv.*, vol. 8, *Gen. Harpe*, p. 9, pl. 3, fig. 5; 1843, Reeve, *Conch. Icon.*, vol. 1, *Harpa*, pl. 1, figs. 1a, b, c. Not *Harpa nobilis* Lamarck, 1816.
- 1807 *Harpis nobilis* Link. *Beschreibung Naturalien-Sammlung Univ. Rostock*, p. 114.

1948 *Harpa harpa* (Linné), M. Smith, Triton Helmet and Harp Shells, p. 48, pl. 16, figs. 3, 6; 1963, Shikama, Selected Shells of the World, pl. 77, fig. 1.

Nomenclature—Under the name *Buccinum harpa* Linné included all the species of *Harpa* then known to exist except *H. costata*. His brief diagnosis is very generalized, and his references are illustrative of five Indo-Pacific species. Of the twelve figures to which reference is made six are referable, either with certainty or probability to the shell which until relatively recently was called *Harpa nobilis* Lamarck.

Although Hanley as early as 1855 (*Ipsa Linnaei Conchylii*, p. 215) concluded that the Linnaean name should be restricted to this form, the first person to use Linné's trivial name for this species appears to have been Maxwell Smith in 1948.

Of historical interest is the fact that Schumacher had given the name *musica* to this species; two specimens bearing this manuscript name were found by me in the collection of the Zoological Museum in Copenhagen.

Types—In the Linnean Collection in London I found the three specimens mentioned by Hanley—one each of *Harpa "nobilis, ventricosa and minor"*. Of these, the first has the word "harpa" written in pencil in the inside, possibly by James E. Smith (see Dance, 1967, p. 8), and is the one I designate here as lectotype. It measures 52 mm. in length and 33 mm. in width.

Records—SOMALIA: Candala (MCZ). MAURITIUS: Gris Gris Beach (Colln. E. Couacaud). ANDAMANS: N end Invisible Bank, in 75 fms. (ANSP). JAPAN: Okinawa, Ryukyus (ANSP, USNM); (Specimens labeled as from Kii, Japan (ANSP) are probably from the Ryukyus). PHILIPPINES: Calapan, Mindoro (ANSP, MCZ); Boac, Marinduque (DMNH); Ticao (AMNH); Borongan, Samar (ANSP); Cebu City, Cebu (AMNH, ANSP); Tabuan, Mindanao; Sarangani Id., Mindanao (both USNM); Zamboanga, Mindanao (AMNH, DMNH); Siasi Id., Siasi Archipelago (MCZ, USNM). INDO-

NESIA: Malawili Channel, North Borneo (Coll. M. Saul); Madura (RNHL); Sanur, Bali (AMNH); Lantutuka, Flores (RNHL); Ambon (AMNH, ANSP, MCZ, RNHL); Wabai, Ceram (BM); Halmahera; Kai Besar; Japen Id., Geelvink Baai, W. Irian (all RNHL); Kepulauan Auri, Geelvink Baai, W. Irian (ANSP). AUSTRALIA: QUEENSLAND: NE Herald Cay, Swains Reef (AMS); Sand Cay No. 8, Queensland (DMNH). PAPUA-NEW GUINEA: Admiralty Ids. (BM); Rabaul, New Britain (AMNH). SOLOMONS: Ataa Id., Malaita (AMNH); Shortland Id., Bougainville (ANSP). FIJI: Nadi Bay, Viti Levu (AMS); Lau Ids. (MCZ). SAMOAN ISLANDS: (BM). TONGA: Tongatapu (Colln. H. C. Gay). MARIANAS: Saipan (ANSP); Guam (USNM). PALAU ISLANDS: Kayangel (BPBM). CAROLINE ISLANDS: Losap Ids. (DMNH). MARSHALL ISLANDS: Boken Id., Taka, Righi Id., Eniwetok; Lomuilal Id., Rongelap (all USNM). GILBERT ISLANDS: (MCZ).

Harpa tosa Aoki, 1966

(Pl. 210)

Range—Lower Pliocene (or Upper Miocene) of southern Shikoku, Japan (Nobori Formation).

Remarks—This species appears to be closest to *Harpa harpa* (Linné) but the upper portion of the body whorl is more rounded and not angulate. The ribs are also less spinose.

Description—The original description reads as follows:

Only one, rather well-preserved and almost complete specimen was collected. It is somewhat deformed transversely due to the diagenesis.

Shell moderate in size for the genus, vertically elongate, subovate, tumid and rather stout, height about 7 cm. maximum width about 4 cm. at the upper one third of the shell, consisting of about five whorls rapidly increasing in size; protoconch relatively small and compressed globose in shape; spire very low and bluntly pointed at the apex; body whorl very large, about 5/6 of the size of the shell; longitudinal ribs prominent, regularly arranged, thirteen in number at the body whorl, flat-topped and wide, running parallel to the growth lines; interspaces wider than ribs, posterior edges of ribs tending to pointed nodes at the shoulder, earlier five ribs of the body whorl covered with callus layer extending from the inner lip, becoming round-topped, weak and somewhat indistinct; growth lines fine but distinct on the ribs and interspaces; no spiral ornamentation present; aperture large and wide, subquadrangular in shape, more than 4/5 of the height [sic] of the shell, inner surface smooth, covered with a thick callus layer; outer lip rather thick; columella nearly straight, fold nothing; canal short and wide, somewhat recurved.

Holotype, Saitama Univ., Paleont. Coll., Reg. no. 11245; from a hill-side cliff, at Minami-habuki,



Plate 210. *Harpa tosa* Aoki, 1966. Lower Pliocene of Japan. 70 mm. (from Aoki, 1966, pl. 31, figs. 12a, 12b).

Nishinohama, Hanemachi, Muroto City, Kochi Prefecture; Nobori formation, Upper Miocene or Lower Pliocene.

Synonymy—

1966 *Harpa tosa* Aoki, Trans. Proc. Palaeont. Soc. Japan, n.s., no. 62, p. 257, pl. 31, figs. 12 a, b.

Harpa amouretta Röding, 1798

(Pls. 183, 189, figs. 6-11; Pl. 211)

Range—Red Sea and East Africa to Hawaii and Marquesas.

Remarks—This species is the most widely distributed of all species of *Harpa* and is found almost throughout the whole Indo-Pacific region. It is also the most variable in shape.

Harpa amouretta is distinguished from most other species by its smaller size, broadly to narrowly ovate shape, by the numerous fine chestnut lines on the ribs, and by the three widely separated blotches on the ventral surface, the central one, near the juncture of the columellar and parietal lips being the largest, the other two—at the upper end of the parietal lip and basal end of columellar lip being small and sometimes absent. It is most closely related to *Harpa gracilis* Broderip and Sowerby and to *Harpa harpa* Linné. From the former it differs in being larger, heavier, broader, and in possessing a pink or pale reddish rather than white protoconch; *H. harpa* is larger, broader, more inflated at the shoulder, with larger ventral blotches, and a peripheral row of irregular blotches on the body whorl.

The species exists in two principal forms; one is stout, strongly shouldered, rather heavy, often rather pale in color, and the other, more slender,

elongate, rather thin, and usually darker in color. The first form, often called *crassa* Mörch, is actually what Lamarck called *Harpa minor* (see below, under "Types"). It is the predominant form in the western Indian Ocean and is apparently the only form found in the Red Sea, but it is also found not infrequently in Micronesia and Melanesia. The other, more slender form is what Röding called *amouretta* and is common in the Pacific, but occasionally found also in the western Indian Ocean. I attempted to separate the two forms as distinct species with possibly distinct but overlapping geographical ranges, but found so much variation and intergradation without any real geographic differentiation in this complex, that I am uniting all under the earliest name, *Harpa amouretta* Röding.

Harpa solidula A. Adams, though not strongly shouldered, represents the stout, solid form; *H. virginalis* 'Gray' Sowerby seems to be a somewhat abnormal form of the "*crassa*" form with a peculiarly attenuated base.

Habitat—This species has been found living in both shallow and deep water. In Ceylon it was found crawling in sand on a reef in 3 inches of water (George Kline, in sched.). R. L. Sixberry, in his field notes, says that this species was found in Baie Taiohae, Nuku Hiva, Marquesas, at night and at low tide in reef flat tidal pools with maximum depths of 3 feet; it was found only on three consecutive nights so it may have been spawning when collected. On Vaitapu, Ellice Islands, Sixberry found it abundant on the reef flat at night in 0 to 6 inches of water. In the 1967 "Pele" expedition, we collected it in 5 to 15 feet of water under coral in Anse Hakapaa, Baie du Controleur, Nuku Hiva, Marquesas. In Hawaii the species apparently lives in deeper water than is usually the case elsewhere; here it has been found in 60 to 65 feet in sand under coral; it apparently spends most of its time buried in the sand with only the siphon visible (Adams, 1966, pp. 2, 5; Harrison, 1968, p. 1).

Description—Shell 20 to 60 mm. ($3/4$ to $2\ 3/8$ inches) in length, varying from narrowly to broadly oval, moderately thin to solid and heavy, basally more or less effuse, body whorl large, spire conical, relatively large (25 to 37% of total length as compared to 21 to 23% for species such as *H. major* and *articularis*). Protoconch rather narrowly conical, consisting of 4 to 5 rounded, basally keeled, glassy whorls flesh pink to strong purplish red. First postnuclear whorl rounded, with numerous spiral cords crossed by strong axial, sub-

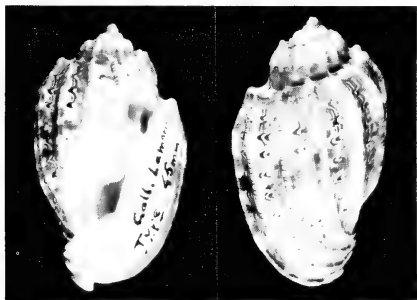


Plate 211. *Harpa amouretta* Röding. Holotype of *Harpa minor* Lamarck, 1822. Muséum d'Histoire Naturelle (Genève). 45.6 mm. in length.

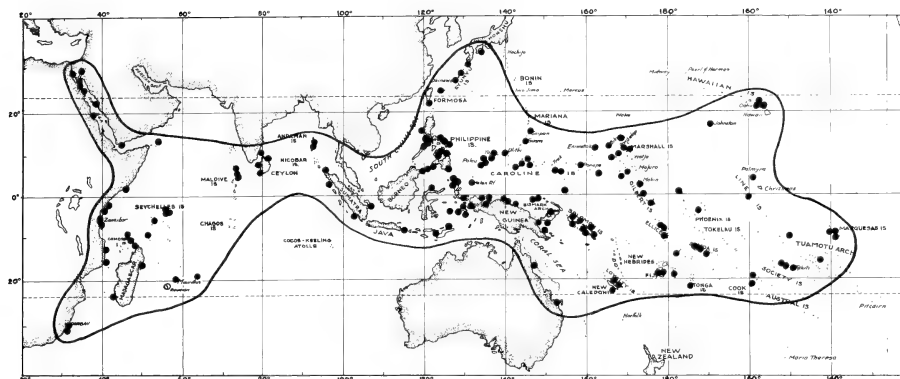


Plate 212. Geographical distribution of *Harpa amouretta* Röding.

lamellar ribs which are only weakly or not at all angulate at the shoulder; only the lower third or fourth of the whorl is covered by the arcuate flattened extension of the axial lamellate ribs of the succeeding whorl. Succeeding postnuclear whorls become more angulately shouldered with the spiral cords restricted to below the shoulder, and the axial ribs become increasingly more lamellar, and strongly angulate and subspicose at the shoulder; the callus formed by the anterior extension of the axial ribs of the succeeding whorl increasingly covers more of the whorl until it may cover more than half of the surface. The body whorl, below the subsutural angle or shoulder may be gently rounded ("*amouretta* form") or broader and subangulate below the shoulder ("*crassa* form"); the ribs, 11 to 15 in number (average 12.5) are triangular in cross-section, occasionally broadened towards the apertural lip, and the interspaces are faintly spirally striate and marked by fine axial growth striae. Ground color of shell very pale yellowish white to deep straw yellow; strongly marked in the intercostal spaces with chestnut brown in varying shades (shells from certain areas, such as the Marquesas have a very dark overall coloration) and in varying patterns, generally of a festooned, zigzag pattern, with irregular splotches, all usually in a basically banded arrangement; in the earliest postnuclear whorls the coloration is restricted to subsutural spots of chestnut which in later whorls tend to become large blotches. The ribs are marked by numerous fine spiral lines in pairs, these pairs usually grouped together and often with darker ground color between them and giving an overall

banded pattern to the whorl. Aperture narrowly ovate, posteriorly more or less acuminate, anteriorly (or basally) rather effuse; outer lip heavy (in the *crassa* form) or rather thin (in the *amouretta* form), not thickened within; inner lip gently arcuate or almost straight, parietal wall covered with a thin glaze which is heavier over the columellar area, extending over the upper part of the strong siphonal fasciole. The inner lip is usually marked by two or three chestnut blotches, one at the juncture of the parietal and columellar lips, one near the juncture with the outer lip, and the other at the base of the columellar lip near the anterior canal; the latter is the smallest and is almost always present, the middle one is usually present but varies greatly in size and shape, and the uppermost one is often absent, especially in the "*amouretta*" form.

The animal is occasionally darker in coloration than in *major* and *ventricosa* and a specimen from the Marquesas shows strong crowded vertical grooves on the anterior margin of the propodium.

Measurements (mm.)—

length	width	no. whorls	
59.7	31.8	7½	large; Lubang, Philippines
52.2	28.8	7½	large; Samar, Philippines
48.6	28.9	7	large; Zanzibar
38.8	22.4	7	medium; Kapingamarangi, Carolines
37.1	24.7	6½	medium; Mauritius
33.6	20.6	6½	medium; Satawan, Carolines
29.8	16.7	7	small; Sumatra, Indonesia
22.7	13.0	6½	small; Seychelles
20.3	10.7	5½	small; Jaluit, Marshalls

Synonymy—

- 1798 *Harpa amouretta* Röding, Museum Boltenianum, p. 150; refers to Martini, Conchylien—Cab., vol. 3, p. 421, pl. 119 fig. 1097 (Amboina); 1938, Adams and Leloup, Res. Sci. Voyag. Indes Orient. Néerl., vol. 2, fasc. 19,

- p. 193; 1939, Peile, Proc. Malac. Soc. London, vol. 23, pp. 271-272, fig. 40 (radula); 1948, M. Smith, Triton, Helmet and Harp Shells, p. 46, pl. 16, fig. 1; 1958, Tinker, Pacific Sea Shells, ed. 2, p. 162, fig.; 1962, Kira, Shells of the Western Pacific in Color, p. 50, pl. 32, fig. 16.
- 1807 *Harpalis amoretta* Link, Besch. Nat.—Sammlung Univ. Rostock, pt. 3, p. 114.
- 1817 *Harpa oblonga* Schumacher, Essai Nouv. Syst. Hab. Vers Test., p. 208; refers to Martini, Conch.-Cab., vol. 3, fig. 1097.
- 1822 *Harpa minor* Lamarck, Hist. Nat. An. s. Vert., vol. 7, (Indian Ocean), p. 257; 1833, Quoy and Gaimard, Voyage Astrolabe, Zoologie, vol. 2, p. 620, pl. 42, figs. 5-7 (animal); 1835, Kiener, Spec. Gen. Icon. Coq. Viv., vol. 8, Gen. Harpe, p. 10, pl. 6, fig. 6a; 1843, Reeve, Conch. Icon., vol. 1, *Harpa*, pl. 3, figs. 6a, 6b; 1853, Chenu, Illustr. Conch., vol. 4, (pt. 85) pl. 2, figs. 5-7; 1857, Kuster, Neues Syst. Conch.—Cab., ed. 2, vol. 3, pt. 1B, pp. 91-92, pl. 67, figs. 6, 7; 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, pp. 115-117; 1883, Tryon, Man. Conch., vol. 5, p. 99, pl. 41, fig. 69-72, 78.
- 1848 *Harpa crassa* "Philippi" Krauss, Südafrikanische Moll., p. 119 (South Africa); 1852, Mörch, Cat. Conch. Yoldi, fasc. 1, p. 125; refers to Martini, Conch.—Cab., vol. 3, pl. 119, fig. 1095; 1860, Sowerby, Thes. Conch., vol. 3, p. 171, pl. 233, figs. 30-31; 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, pp. 117-119.
- 1854 *Harpa solidula* A. Adams, Proc. Zool. Soc. London, pt. 21, p. 173, pl. 20, figs. 9-10.
- 1857 *Harpa gracilis* Brod. and Sby., Küster, Neues Syst. Conch.—Cab., ed. 2, vol. 3, pt. 1B, p. 91 (in part), pl. 67, figs. 4, 5. Not *gracilis* Brod. and Sby., 1829.
- 1870 *Harpa virginialis* Gray Sowerby, Thes. Conch., vol. 3, p. 172, pl. 233, figs. 34, 35; 1883, Tryon, Man. Conch., vol. 5, p. 99, pl. 71, fig. 78 (as syn. of *minor* Lam.).
- 1860 *Harpa solidula* A. Ad., Sowerby, Thes. Conch., vol. 3, p. 172, (as syn. of *crassa* Mörch; error for *solidula* A. Ad.).

Types—*H. amouretta* Röding was based on a specimen described and figured by Martini from his collection; the present location of this specimen is not known. The type locality is Ambon, Indonesia.

The holotype of *Harpa minor* Lamarck is in the Natural History Museum of Geneva (Plate 211), and represents the heavy shouldered form; it measures 45.6 mm. in length. Of the four specimens of this species in the Lamarck Collection in Geneva, three are of the *crassa* form, and one of the *amouretta* form.

The type of *Harpa crassa* "Philippi" Krauss is not present among what remains of Krauss' collection in the Museum of Natural History in Stuttgart (see Janus, 1961). Three syntypes of *Harpa crassa* Mörch, 1852, which Mörch listed as a new taxon, are present, on the other hand, in the Zoological Museum in Copenhagen; the largest specimen, which is worn, measures 35.5 mm. in length, the other two 33.5 and 33 mm. I designate the one measuring 33.5 mm. as the lectotype. Since the original label bears the locality data "Isle de Fr.," the type locality should be Mauritius.

Harpa solidula A. Adams is represented in the British Museum Collection by three syntypes originally glued on a tablet and belonging to the Cuming Collection. Of these the smallest and most vividly colored one agrees quite closely with the original figure, and so I designate it as the lectotype; it measures 33.5 mm. in length and 20 mm. in width.

The whereabouts of the type of *Harpa virginialis* Gray Sowerby is not known.

Selected Records (for additional records see map)—SOUTH AFRICA: off Durban, Natal, from fish stomach (DMNH); Umtwalumi, 22 mi. N of Port Shepstone, Natal (ANSP). MOZAMBIQUE: Porto Amelia (AMNH, USNM); Moçambique (USNM). TANZANIA: Latham Id., 50 mi. E of Dar es Salaam (Colln. Vokes); 4 mi. N of Dar es Salaam (MCZ); Bawe Id., 4 mi. NW of Zanzibar City (USNM); Ras Kizimkazi, SW Zanzibar (ANSP). KENYA: 16 mi. S of Mombasa (ANSP); Tiwi (MHNG); 4 mi. SE of Gedi, Kilifi Distr. (AMNH). SOMALIA: Mogadiscio (AMNH, ANSP, USNM). SOCOTRA: North Coast (ANSP). RED SEA: Gulf of Suez (BM, MCZ); Eilat, Gulf of Aqaba (AMNH, BM, TAU); Ras Muhammed, S tip Sinai (TAU); Dishet ad Dab'ah, Egypt (RNHL); E of Jabal Zabarrah, Egypt (ANSP); 40 km N of Jidda, Saudi Arabia (AMNH); Jidda (RNHL); Port Sudan, Sudan (AMNH, MCZ). ADEN: (BM). MADAGASCAR: Nosy Bé (ANSP, MCZ, RNHL); NW of Ambodifotra, Ile Ste. Marie; Grande Réféc, Tulear (both MCZ); SEYCHELLES: Anse Boileau, W Mahé (ANSP, BM); 1 mi. S of Anse aux Pins, SE Mahé; Curieuse Id. (both ANSP); La Digue (BM). MAURITIUS: Flie-en-Flacq; Nr. Black River (both ANSP). LA REUNION: (Deshayes, 1863). INDIAN OCEAN ISLANDS: Darros Id., Amirante Isles (BM); St. Josephs Ids., Amirantes (Colln. Vokes); Iles Glorieuses; Providence Id. (both USNM); West Id., Aldabra (Colln. Vokes); Rodrigues (BM). MALDIVES: Fadiffolu Atoll; Tildumattati Atoll; N. Malosmadulu Atoll (all ANSP); CEYLON: Galle Beach (AMNH, BM); Fort Frederick, Trincomalee; Hikkaduwa (both ANSP). INDIA: Tranquebar (ZMC). ANDAMAN ISLANDS: Bonnington; Long Id.; Port Blair (all BM); JAPAN: S coast Shikoku and southwards (Kira, 1962); Osumi Gunto, Ryukyu Ids. (MCZ, USNM); Naha, Okinawa, Ryukyu Ids. (ANSP); Taketomi Shima, Ryukyu Ids. (BPBM). TAIWAN: (USNM); Oluan Pi (ANSP). PHILIPPINES: Batangas Bay, Batangas, Luzon (AMNH); Botolan, Zambales, Luzon (ANSP); Gigmoto, Catanduanes (ANSP, DMNH); Tilig Bay, Lubang (ANSP); Pola, Mindoro (AMNH); Calapan, Mindoro (MCZ); Culion (AMNH); Capul, NW Samar (ANSP); Borongan, E Samar (ANSP, DMNH, MCZ, USNM); Cebu City, Cebu (ANSP, DMNH); Panglao Id., Bohol (AMNH); Davao, Mindanao (MCZ, USNM); Zamboanga, Mindanao (ANSP, DMNH, USNM); Pt. Matangal, Basilan; Jolo City, Jolo (both USNM); Siasi, Sulu Archipelago (AMNH, DMNH); SW end Sanga Sanga Id. (ANSP). INDONESIA: Pulau We, N Sumatra (RNHL); Pulau Penjoe, Pulau Simeulue, W Sumatra (USNM); Pulau Bali, W Sumatra; Bengkulu, S Sumatra; Bangka (all RNHL); Bali (BPBM, MCZ); Timor; Wetar; Bandanaira, Banda; Lintido, Celebes (all RNHL); Busak, N Celebes; Karakelong, Kepulauan Talaud; Pulau Dagasul, Loloda Utara, Halmahera (all MCZ); Pulau Tenga, Buru; Manipa, W Ceram (both RNHL); Pulau Boana, Ceram (ANSP); Ambon (ANSP, MCZ, RNHL); Waihai Ceram (BM). INDONESIA: WEST IRIAN: Pulau Gam (MCZ); Fakfak; Manokwari (both MCZ); Pulau Maransabadi, Kepulauan Auri; Soepiori, Kepulauan Schouten; Biak, Kepulauan Schouten (all Geelvinck Baai, and ANSP); Pulau Nukori, Kepulauan Padidao, Geelvinck Baai (USNM); Insumanai, Kepulauan Wakde (MCZ); nr. Hollandia (USNM). PAPUA-NEW GUINEA: Seleu Id., Aitape; Finschhafen (both MCZ); Oro Bay (ANSP). QUEENSLAND: Tin Can Bay (MCZ); Green Id.

(AMNH). ADMIRALTY ISLANDS: Manus Id. (MCZ); Koruniat Id. (ANSP); Los Negros Id. (USNM). NEW BRITAIN: Kumbun Id., nr. Kandrian (ANSP); Rabaul (AMNH, ANSP); Blanche Bay (RNHL). SOLOMON ISLANDS: Kieta, Bougainville (AMNH); Shortland Id. (ANSP); Treasury Ids. (USNM); Choiseul Bay, Choiseul (AMNH); Roviana, New Georgia (MCZ); Pavuvu Id., Russell Ids. (USNM); Ataa, N Malaita (AMNH); Ugi (USNM). NEW CALEDONIA: 2 mi. SSE of Toutho (ANSP); Noumea (MCZ). LOYALTY ISLANDS: Lifu (AMNH); Fijie, Korolevu, Viti Levu (ANSP); Mbengga, S of Viti Levu (USNM); Lau Ids. (MCZ). HOORN ISLANDS: Anse de Sigave, Futuna (USNM). SAMOAN ISLANDS: Asau Harbour, Savaii; Apia, Upolu; nr. Matautu Pt., Apia, Upolu (all USNM); Tutuila (ANSP); TONGA: Tongatapu (MCZ, USNM). MARIANA ISLANDS: Agrihan; Saipan; Port Merizo, Guam (both ANSP); Agaña Bay, Guam (ANSP, BPBM); Cocos Id., S of Guam (ANSP). PALAU ISLANDS: E Babelthup (ANSP, MCZ, USNM); reef off Airai, Babelthup; Malakal Harbor; N side Ngarapala, Kayangel Islets (all ANSP). CAROLINE ISLANDS: Round Rock, Helen Reef (ANSP); Ngulu Atoll (USNM); Yap (ANSP, USNM); Ulithi Atoll; Fassarai Ids., Ulithi Atoll; Eauripik Atoll; Falarik Id., Ifalik Atoll; Faraulp Atoll; Elato Atoll (all USNM); Lamotrek Atoll (BPBM, USNM); Satawal Id.; W side Oneop Id., Lukunor Atoll; Satawan Atoll; Kapingamarangi Atoll; Touthou Id., Kapingamarangi Atoll (all USNM); Losap Ids. (DMNH); Ponape (ANSP, BPBM, MCZ); Mutunlik, Kusaie (USNM). MARSHALL ISLANDS: Rujuru Id., Eniwetok; Aramit Is., Eniwetok; Namu Id., Bikini; Yomyaran Id., Bikini; Bock Id., Rongerik; Lato-back Id., Rongerik; Wotho; Bigenkai Id., Ujae; Torrutj Id., Kwajalein; Mejjatto Id., Jaluit (all USNM); Ebon (MCZ, USNM); Bikar; Boken Id., Taka; (both USNM); Likiep (BPBM); Meijbin Id., Majuro (USNM); Arno (AMNH). GILBERT ISLANDS: Abaang (MCZ); Abemama; Onotoa (both USNM). ELLICE ISLANDS: Vaitupu (USNM); Funafuti (MCZ); Nukulaelae (USNM). HOWLAND ISLAND: (ANSP, MCZ). PHOENIX ISLANDS: Canton (BPBM). EASTERN POLYNESIA: CAROLINE ISLANDS: Fanning; Jarvis (both DMNH); Caroline Atoll (ANSP, USNM). COOK ISLANDS: betw. Black Rock and Nikao, NW Rarotonga (ANSP, MCZ); Avatiu Harbor, Rarotonga; Manuae, Hervey Ids. (both USNM). SOCIETY ISLANDS: Patutote, Papeete, Tahiti (USNM); Vairahi Bay, Raiatea; (ANSP); Tahaa (DMNH); Bora Bora (both ANSP). TUA-MOTU: Takume (USNM). MARQUESAS ISLANDS: Baie Taiohae, Nuku Hiva (DMNH, USNM); Anse Hakapaa, Baie du Contrôle, Nuku Hiva (USNM); Baie Hanahevana, Ta-

huata; Baie d' Hananai, Ua Huka (both ANSP). HAWAIIAN ISLANDS: Waikiki, Oahu (T. Richert Colln); Waimanalo Bay, Oahu (MCZ); Honolulu Harbor (USNM); Kaanapali, Maui (Colln. R. Gage). JOHNSTON ISLAND: Sand Island (USNM).

Fossil records—INDONESIA: near Kajoe Raji, N Celebes; age: Pleistocene (Schepman, 1907, p. 164). MARIANAS: 1650 ft., E by S of Mt. Almagosa, Guam, in Talisay member of Alifan limestone (USGS 20640); age: Upper Miocene (Tertiary g) or Pliocene (Tertiary h). HAWAIIAN ISLANDS: 40-50 ft. alt., lava cliff, Kapihaa Bay, Lanai; age: Pleistocene (Y. Kondo, BPBM); 250-290 ft. alt., Kawai Stream, Lanai (USGS 13918); age: Pleistocene (H. T. Stearns, USNM). PHOENIX ISLANDS: emergent reef (2600 years old), Enderbury Island (J. I. Tracy, Jr., USNM).

Harpa gracilis Broderip and Sowerby, 1829

(Pl. 189, figs. 3-5)

Range—Ellice Islands to the Tuamotus and Clipperton Island.

Remarks—This small and distinctively characterized species is still rare in collections. From small elongate specimen of *H. amouretta* it can be differentiated by possessing a narrow umbilicus, a more slender shape, higher spire, white protoconch, more slender ribs not angulate at the shoulder, and an anteriorly more effuse aperture.

Sutor (1877) records *gracilis* from Rarotonga in the Cook Islands and the Gilbert Islands. The former locality needs verification, and from Abemama in the Gilbert Islands and Vaitupu in the Ellice Group I have seen narrow, rather thin specimens that have a resemblance to *gracilis* but are definitely *Harpa amouretta*. Hedley (1899) records the species from Funafuti, Ellice Islands, and I have seen two specimens from this atoll.

During a visit to Clipperton Island in 1959 of the Scripps Oceanographical Institute research vessel "Downwind," a specimen was collected by E. A. Allison on the beach. I have been able to examine the two specimens collected on Clipperton during the French "Bougainville" Expeditions, 1966-1968 (Salvat and Ehrhardt, 1970, p. 226).

This wide but scattered distribution is interesting, but further intensive collecting in the Northern Cook Islands and the Line Islands may reveal its presence there. It is difficult to explain its occurrence in Clipperton, as we know nothing of the early stages of development in the genus.

A specimen in the Delaware Museum of Natural History is said to have come from a coral reef at low tide off Papeete, Tahiti. Its presence on a high island (all other known specimens are from coral atolls) is suspect, and as the collector is unknown, I am treating this record as doubtful.

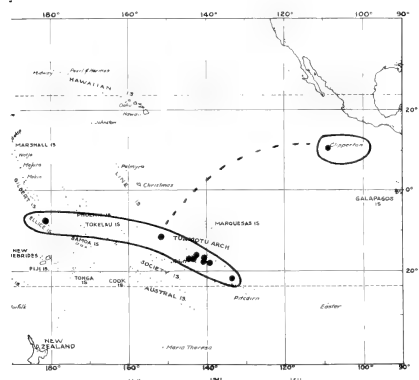


Plate 213. Geographical distribution of *Harpa gracilis* Broderip and Sowerby.

Description—Adult shell 25 to 29 mm. (1 to 1 1/8 inches) in length, narrow-elongate, basally somewhat effuse, with a moderately high conical spire. Nuclear whorls 3 1/2 to 4, smooth, white, early postnuclear whorls white or pale rosy-white, marked by evenly spaced low retractorily curved axial ribs, the interspaces marked by fine spiral lirae that run up onto the apertural edge of the ribs; ribs on penultimate whorl marked by transverse lines of chestnut brown, becoming obscure where they are covered by the parietal callus glaze. On body whorl the ribs are low, flattened, of varying width, marked by chestnut-brown lines usually arranged in groups of three or four; the ribs on the ventral side appear to vanish under the thin parietal glaze which at the lower end partially covers the siphonal fasciole and the narrow umbilicus. Aperture elongate, narrow at the posterior end, broad at the anterior end.

Measurements (mm.)—

length	width	no. whorls	
35.4	16.5	—	large; Tuamotus
29.2	14.5	6	large; Anaa, Tuamotus
27.6	13.1	6	average; Vahitahi, Tuamotus
26.4	12.9	4½	average; Flint Id., Line Ids.
20.8	10.2	5	small; Raroia, Tuamotus
24.4	11.3	6½	small; Funafuti, Ellice Ids.

Synonymy—

- 1829 *Harpa gracilis* Broderip and Sowerby, Zool. Journal, vol. 4, p. 373 (no locality; type locality here designated as Vahitahi, Tuamotus); 1843, Reeve Conch. Icon., vol. 1, Harpa, pl. 2, fig. 3a, b (Anaa Id.); 1860, Sowerby, Thes. Conch., vol. 3, p. 171, pl. 233, figs. 32, 33; 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, pp. 120-121; 1883, Tryon, Man. Conch., vol. 5, p. 99, pl. 41, fig. 73; 1899, Hedley, Mem. Austral. Mus., vol. 3, p. 470; 1907, Coutourier, Journ. de Conchyl., vol. 55, p. 132; 1933, Dautzenberg and Bouge, Journ. de Conchyl., vol. 77, p. 149-150.
- 1839 *Harpa minor* B. *gracilis* Brod. and Sby., Gray, Zool. Capt. Beechey's Voyage, p. 122, pl. 36, fig. 17 (Pacific Ocean).
- 1948 *Harpa amouretta gracilis* Brod. and Sby., M. Smith, Triton Helmet and Harp Shells, p. 46.

Types—According to the original authors the species was described from a single specimen collected by Lt. Belcher while on the voyage of the "Blossom" under Captain Beechey, and at that time in "Mr. Bland's collection." The whereabouts of this collection and the type of this species are unknown; it may be the same collection as that listed by Sherborn (1940, p. 19) as "Mich. Bland," a collection he states was sold at auction in May 1851. According to Rosewater (1968, p. 351) the "Blossom" visited thirteen atolls in the Tuamotus. Of these I designate Vahitahi as the type locality. Anaa, the atoll where Cuming collected the specimen figured by Reeve, was not visited by the "Blossom."

Records—ELLICE ISLANDS: Funafuti (AMS). SOUTHERN LINE ISLANDS: Flint Id. (ANSP). TUAMOTUS: Anaa (AMNH, ANSP, BM); Raroia; Vahitahi (both USNM); North Marutea; Amanu, Hao, South Marutea (all Seurat, in Dautzenberg and Bouge, 1933). CLIPPERTON: (CAS, MHNP).

Harpa kajiyamai new species, Rehder

(Pl. 188, figs. 3, 4)

Range—The southern Philippines.

Remarks—It is remarkable that this rather striking species has been unrecognized as distinct for so long. In 1966 Habe and Kosuge (Shells of the World in Colour, vol. II: The Tropical Pacific, p. 79, pl. 30, fig. 3) described this shell as *Harpa cancellata* Röding, 1798. They call attention to its rather narrow form, and the thinness of the glaze on the parietal wall. It is of course not *H. cancellata* Röding, which I consider a synonym of *H. davidis* Röding. Dr. Habe in a letter to me said he had recognized that the species in question was new, and had given it a provisional new name. Upon my request Dr. Habe very generously sent me three specimens of this species that had been loaned to the National Science Museum in Tokyo, and is permitting me to describe this species. At his request I am naming it for Mr. Hikotaro Kajiyama who brought these specimens to Dr. Habe.

The most obvious characters that differentiate it from related species is the rather elongately ovate shape and the presence of only a thin glaze on the parietal wall with two chestnut brown spots on the ventral side—a larger, elongate one at the base of the parietal wall above the upper end of the siphonal fasciole, and a small one near the base of the columellar; occasionally there may be small spot on the parietal wall near the junction of the outer lip.

Its closest relative in some aspects is *Harpa amouretta* in the thinness of the glaze on the parietal wall, the spot at the base of the parietal wall, and in the presence of numerous transverse dark lines on the ribs. It is, however, more ovate, with a lower spire, and a larger spot at the base of the columellar wall. In this respect it is more like *H. major*. It is larger than *H. amouretta*.

Description—Of moderate size, adult shells 67.7 to 72.4 mm. (2½ to 2¾ inches) in length, ovate, with body whorl convex but medially slightly flattened, spire moderately high, conical. Protoconch erect-mamillate, pale yellowish pink to light pink, with 3¼ to 3½ smooth, convex whorls, with medial keel rather prominent; usually somewhat tilted. Early postnuclear whorls with distant axial ribs and a rather strong spiral ridge at the shoulder and one or more visible below the shoulder; the area

of the whorls covered by the procurved upper ends of the ribs of the succeeding whorl increases rapidly so that in the latter half of the second post-nuclear whorl, the callus covers all of the whorl below the subsutural shoulder, and in the last two whorls even the shoulder is covered; the axial ribs (17 to 19 in penultimate whorl) bear a strong triangular spine at the shoulder angle; the subsutural ramp is smooth. Body whorl ovate, slightly flattened medially, with 14 to 17 ribs which are sharply acuminate at the shoulder angle, smooth below, and flattened and reflected, strongly reflected at base towards the strong siphonal fasciole where the ends of the ribs are conspicuous and flattened; the subsutural ramp is very finely axially sculptured by microscopic irregular growth lines which become obsolete below the shoulder between the ribs where they are replaced by stronger, separated axial threads, crossed by numerous fine, low spiral ridges of irregular strength, with occasionally more pronounced ones among them. The parietal wall is covered by a thin transparent glaze, which becomes thicker towards the siphonal fasciole and over the columellar area, covering the inner part of the fasciole. A large, elongately curved, dark reddish brown to grayish reddish brown spot is situated at the base of the parietal wall just above the upper part of the light yellowish brown siphonal fasciole; a small spot of the same color is situated on the columella above the anterior tip which is grayish yellow; occasionally this dark spot extends up on the columellar to below the siphonal fasciole. Occasionally a small or obscure spot is present on the parietal wall near the juncture with the outer lip. Outer lip evenly arcuate, not much thickened, marked by the ends of the spiral banded coloration of the exterior. The color of the exterior of the shell is vivid and of the typical *Harpa* pattern, the darker spots on the ribs being marked by seven groups of horizontal dark lines, usually in pairs or triplets. Occasionally a spiral series of irregular splotches of moderate reddish brown is present in the middle section of the body whorl. The anterior siphonal sinus is broad and open.

Measurements (mm.)—

length	width	no. whorls	
72.4	48.5	7	Holotype
69.8	46.2	7	Paratype no. 1
67.7	41.4	7½	Paratype no. 2

Synonymy—

1966 *Harpa cancellata* Röding, Habe and Kosuge, Shells of the World in Colour, vol. 2: The Tropical Pacific, p. 79, pl. 30, fig. 3. Not *Harpa cancellata* Röding, 1798.

Types and Records—The holotype is in the National Science Museum of Tokyo, no. 41450, while paratype no. 1 is in the collection of Mr. Hikotaro Kajiyama, and paratype no. 2 is in the collection of Mr. Ryosuke Kawamura.

Harpa major Röding, 1798

(Pl. 183; Pl. 188, figs. 8-11; Pl. 214)

Range—East Africa to Hawaiian and Marquesas Islands.

Remarks—This is a very widely-spread species and also rather variable in its color pattern and in the nature of the ribs. It is in general characterized by its rather heavy, oval and not angulate shell, the chestnut blotch on the ventral surface more or less divided in the center of the parietal wall with the lower part continuing down without interruption to the base of the columellar. Specimens of this species vary from those with a generally pale pink coloration, wide ribs and without any dark lines on the ribs to dark forms with numerous dark lines on the ribs.

The species that Sutor (1877, p. 107) described as *Harpa ligata* Menke appears to represent this latter darker form (Sutor calls the coloration "intense") with numerous dark lines on the ribs, a broadly ovate shape with short spire and a generally dark parietal blotch with only a small elongate light area in the middle. The general outline of the shell, height of spire, number of dark lines on the ribs, and the extent of the dark chestnut ventral blotch varies so much in various combinations throughout the range, that no distinct specific or subspecific separation can be made based on these characters. There seems to be a center of

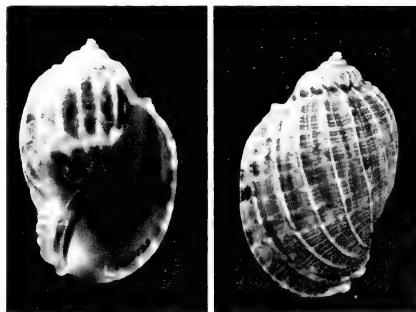


Plate 214. *Harpa major* Röding. Lectotype of *Harpa striatula* A. Adams, 1854. 44 mm. in length. British Museum (Natural History). No. BM 1965-133.

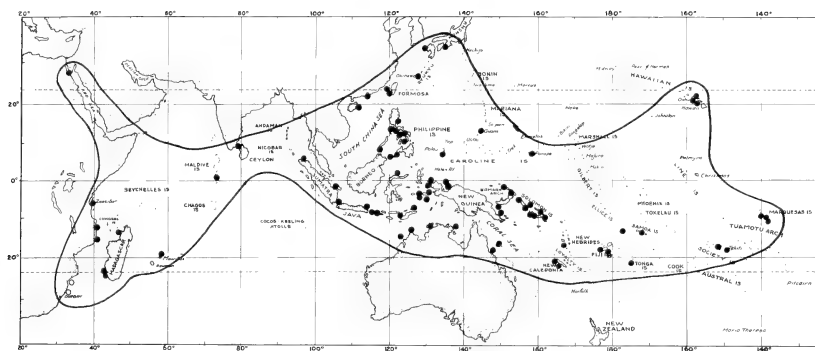


Plate 215. Geographical distribution of *Harpa major* Røding.

deep-colored forms with a more or less solid dark-chestnut blotch on the ventral surface in central Melanesia; I have seen such specimens from the Sulu Archipelago in the Southern Philippines, New Britain, Solomons, and eastern Papua, but as more typical forms are also found in the same area, I consider these dark forms to be merely ecological variations.

I have seen a specimen from Oahu, Hawaii with a pale pink and white ground color on both ribs and interspaces, with strong paired dark lines on the ribs.

Occasional small specimens are found in which the striate sculpture of the intercostal areas, typically found in the juvenile stage, is continued and even conspicuously strengthened in later whorls. On two such specimens, 44 mm. and 50 mm. in length, A. Adams founded his *Harpa striatula* (Plate 214). Oostingh (1938, pl. 7, fig. 144) figures such a shell from the Pliocene of Java.

Habitat—A deeper water shell living on a bottom of sand or sand and rubble. C. S. Weaver mentions (1963, p. 1) having taken a living specimen moving over the sand in 55 to 60 feet of water in Kailua Bay, Oahu, Hawaii. In the Marquesas numerous living specimens were dredged in from 26 to 51 fathoms on bottoms of varying proportions of sand, broken shell and rubble.

Description—Shell 50 to 108 mm. (2 to 4½ inches) in length, broadly oval, usually solid and comparatively heavy, last whorl large, spire broadly conical. Protoconch conical, of 3½ to 4 whorls, rounded, glassy, flesh-colored. Early post-nuclear whorls showing sharp axial ribs and two or three spiral cords, giving those whorls on the spire a cancellate appearance, and the uppermost

one giving these whorls a shouldered appearance with a flattened subsutural area; the color changes from the flesh color of the nuclear whorls to white, often with scattered chestnut spots. In the juvenile shells the interspaces are sculptured with low, broad, and flattened spiral cords, subequidistantly spaced, and crossed by very fine, crowded and sharp axial threads. The last two whorls of the spire are covered with a glaze varying in color from flesh or cocoa color to yellowish and dark coffee color. Body whorl comprises about 90 to 95% of the total shell length, and bears 12 to 16 ribs of varying widths; the ribs are prominently and subspinosely angulate at the edge of the subsutural ramp, the spines on the last whorls giving a channeled appearance to the spire; at the suture the ribs flatten out and coalesce forming a callus that covers the penultimate whorl; between the ribs the surface is axially finely striated. The color of the shell varies from pinkish flesh-color to deep reddish brown with the area between the ribs showing an axially festooned pattern of pink, white or chestnut. There is always some sort of a banded pattern shown that is carried out on the ribs also; the presence or absence of chestnut lines on the ribs is a variable character. The aperture is rather large, ovate, the outer lip simple, gently arcuate with a shallow anal sinus between the spinose angulation and the suture. The lower part of the lip curves away retractively to the rather broad siphonal canal. The columellar lip is bounded by a strong rounded fasciole, lamellosely ridged by the strongly and retractively curved basal ends of the ribs. The whole parietal wall and columellar area is covered with a glaze, which bears a large deep chestnut blotch extending from the suture to almost the end of the columellar lip; in the middle of the parietal wall a narrow or

wedge-shaped light area nearly or completely divides the blotch into two parts. The ribs on the parietal wall are only lightly colored and show through prominently. The basal tip and inner part of the columellar lip is straw-colored or pale brown. The interior of the aperture is largely colored a light brown; near the outer lip it is paler with the color banding often showing through.

Measurements (mm.)—

length	width	no. whorls	
105.3	69.0	7	large: Guam, Marianas
93.6	64.6	6½	large: Cebu City, Philippines
82.5	59.4	6½	average: Ryukyu Islands
69.8	47.2	6½	average: Okinawa, Ryukyu
51.1	32.9	6	small: Okinawa, Ryukyu
48.4	33.7	6	small: Lubang, Philippines

Nomenclature—This species is one of the most variable in the genus and consequently a great deal of confusion has arisen concerning its proper name. Recent workers (Wagner and Abbott, 1967, pp. 115-116) have equated *major* Röding with *ventricosa* Lamarck and *conoidalis* Lamarck with *davidis* Röding, a confusion that dates back to Lamarck who placed references now assigned to *major* under his *ventricosa*. Other workers (Maxwell Smith, 1948, p. 47; Habe, 1961, p. 68) have synonymized *Harpa major* with *davidis* Röding. It is worthy of comment that although the species on which Röding based his *Harpa major* is what Martini in 1777 called "Die grosse Davidsharfe" Röding gave the name *Harpa davidis* to another shell described and figured by Martini in the same volume.

Synonymy—

- 1798 *Harpa major* Röding, Museum Boltenianum, Hamburg, pt. 2, p. 149, no. 1872; refers to Conchyl.-Cab., vol. 3, pl. 119, f. 1090 (East Indies); [The figures of Knorr cited by Röding represent *Harpa* L.]
- 1807 *Harpalis major* Link, Besch. Nat. Samml. Univ. Rostock, pt. 3, p. 114; refers only to Conchyl.-Cab., vol. 3, pl. 119, f. 1090.
- 1811 *Harpa grandiformis* Perry, Conchology, pl. 40, no. 1 (West Indies)
- 1817 *Harpa vulgaris* Schumacher, Essai Nouv. Syst. Hab. Vers Test; p. 208. New name for *Harpa ventricosa* Lamarck in part.
- 1818 *Buccinum harpa* Wood, Cat. Shells, p. 107, pl. 22, f. 49. Not *B. harpa* Linné, 1758.
- 1822 *Harpa conoidalis* Lamarck, Hist. Nat. An. s. Vert., vol. 7, p. 255 (no locality); 1843, Reeve, Conch. Icon., vol. 1, Harpa, pl. 3, f. 7a, 7b, 7c; 1962, Kira, Shells Western Pacific in Color, p. 90, pl. 32, f. 17.
- 1822 *Harpa ventricosa* Lamarck, op. cit., p. 255 (East Indies), in part; 1833, Quoy and Gaimard, Voy. Astrolabe, Zool., vol. 2, p. 611-619, pl. 42, f. 1-4 anatomy (not *H. ventricosa* Lam.); 1843, Reeve, Conch. Icon., vol. 1, Harpa, pl. 1, sp. 2 (in part; fig. 2a only).
- 1828 *Harpa ligata* Menke, Syn. Meth. Moll., p. 86 (no locality); 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, p. 107, pl. 5, f. 2 (Duke of York Ids. [Tokelau Ids.])

- 1835 *Harpa ventricosa* var. *conoidalis* Lam., Kiener, Spéc. Gén. Icon. Coq. Viv., Gen. Harpe, p. 7, pl. 3, f. 4.
- 1835 *Harpa ventricosa* Lam., var., Kiener, op. cit. p. 7, pl. 6, f. 9-10.
- 1835 *Harpa nobilis* Lam., var., Kiener, op. cit., p. 10, pl. 6, f. 11.
- 1854 *Harpa striatula* A. Adams, Proc. Zool. Soc. London, pt. 21 (1853), p. 173, pl. 20, f. 7, 8 (no locality): juvenile.
- 1860 *Harpa nablum* 'Mart.' Sowerby, Thes. Conch., vol. 3, p. 170 (in part), pl. 232, f. 14, 17. Not *H. nablum* Möhrsch, 1853.
- 1961 *Harpa davidis* Röding, Habe, Col. Illustr. Shells, Japan, vol. 2, p. 68, pl. 33, f. 24. Not *H. davidis* Röding, 1798.

Types—The whereabouts of Martini's specimen on which Röding's name is based is unknown. Pending the possibility of the eventual discovery of Martini's specimen, his illustration may serve as a "type figure." The type locality, given as East Indies, I restrict to Ambon.

The type of *Harpa conoidalis* Lamarck could not be found in the museum in Geneva, and may be in existence in France. The types of Menke's *ligata*, and Perry's *grandiformis*, have also not been located.

Two cotypes of *Harpa striatula* A. Adams were found in the British Museum; the smaller one, measuring 44 mm. in length and 29 mm. in width, is the one figured by Adams, and is designated as the lectotype (BM 1965-133).

Records (see accompanying map, pl. 215)—SOUTH AFRICA: off Unvoti River (Barnard, 1959, p. 35). MOZAMBIQUE: Baía de Lourenço Marques (Barnard, 1. c.); Moçambique (ANSP, DMNH); Porto Amelia (USNM). TANZANIA: Zanzibar (AMNH, ANSP); Chambe Id., SW Zanzibar; Pange Id., W Zanzibar; Bawi Id., W Zanzibar; Kuwenga, Zanzibar; Mnemba Id., NE Zanzibar (all ANSP). KENYA: Jidini (BPBM). RED SEA: Strait of Jubal (ANSP). MADAGASCAR: Tulear; Soalara, 16 mi. S of Tulear (both MCZ); 28-34 mi., sandy mud, 32 mi. SW of Nossi Be (ANSP, MCZ). MAURITIUS: (AMNH, ANSP, USNM, RNHL); La Gaulette (USNM); G. Antilene (DMNH). MALDIVES: Hulele (ANSP). INDIA: Rameshwaram, Paniban Id., Madras (USNM). CEYLON: (AMNH, ANSP). JAPAN: Kii, Honshu (AMNH); Tosa, Shikoku; Kashiwa Shima, W. Coast Kyushu (both DMNH); Okinawa, Ryukyu (ANSP, MCZ, USNM). MARIANAS: Guam (USNM); Cocos Id., SW Guam. PALAU ISLANDS: S of Ngergi (both ANSP). CAROLINE ISLANDS: Ponape (MCZ). TAIWAN: off Kaohsiung (AMNH, USNM); off Anping; Pescadores (both ANSP). CHINA: Hongkong (DMNH); S of Lema Ids., Hongkong; 50-100 fms., E of Hainan (both ANSP). PHILIPPINES: Baler, Quezon, Luzon; W Paluan Bay, Mindoro (both USNM); Pola, Mindoro (MCZ); Calapan, Mindoro (AMNH, ANSP, MCZ); Tilig, Lubang, Mindoro (USNM); Silangan Bay, Lubang, Mindoro; Cabra Id., Lubang, Mindoro (both MCZ); Capul Id., NW Samar (ANSP); Capiz, Panay (MCZ); Cebu City, Cebu (ANSP, USNM); Zamboanga, Mindanao (DMNH); Balabac (ANSP); Tubigan Id., Pangutaran Group (USNM); Jolo (ANSP); Laminusa Id., Siasi Id., Sulu Arch. (DMNH), Siasi Id. (MCZ, USNM); Bongao Channel, SW end Sanga Sanga Id., Sulu Arch. (ANSP). INDONESIA: Uelheue, Kutardja, NW Sumatra; Bangka (both RNHL); Keledjitan, Bantam, Java; Tipperwagaram, Bantam, Java (both USNM); Madura; Bali (both RNHL); Ampenan, Lombok (USNM); Timor; Wetar; Banda (all RNHL); Ambon (NCZ, RNHL); Manipa, betw. Buru and Ceram; Ceram; Busak; N Celebes; Waigeo, W Irian; Fak-Fak, W Irian; Sekru, W Irian; Seroei Bay, Japen, W

Irian; Biak, W Irian; (all RNHL). WESTERN AUSTRALIA: SW of Adele Id., off King Sound; off Troughton Island (both WAM); Darwin. NORTHERN TERRITORY: Yirrkala. QUEENSLAND: West Cay Diamond Islets; Palm Island (all AMS). ADMIRALTY ISLANDS: (NMV). BISMARCK ARCHIPELAGO: Tsoi Launung Id., betw. New Hanover and New Ireland (AMS); Duke of York Id. (RNHL); Rabaul, New Britain (AMNH, USNM); Matupit Id., Rabaul, New Britain; Kambulu, New Britain; Gumlung Id., New Britain (all ANSP). PAPUA: Goodenough Id. (AMNH, USNM). SOLOMON ISLANDS: Teop Id., Bougainville (AMNH); Gihili, Bougainville (AMS); Buin, Bougainville (AMS); Buka Id., Bougainville (MCZ); Shortland Id. (ANSP); Senga, Choiseul (AMNH); Kukodo, Gizo Id.; Kilapoda Reef, Vangunu Id., New Georgia (both ANSP); Ususue, Ata District, Malaita (AMNH, ANSP); Ugi Id., San Cristobal (USNM). NEW HEBRIDES: Lamap, Malekula (ANSP). NEW CALEDONIA: Bourail; Koumac (both ANSP). FIJI: Nadi Bay, Viti Levu (AMS); Suva Harbor, Viti Levu (USNM); Lau Ids. (MCZ). WALLIS ISLANDS: (MCZ). SAMOAN ISLANDS: Upolu (ANSP). TONGA: Monuafu Reef, Tongatapu (Colln. H. C. Gay); Niuatoua Reef, Tongatapu (USNM). SOCIETY ISLANDS: Mataiea, Tahiti (ANSP); motu S of Faaroa Pass, Raiatea (DMNH). MARQUESAS ISLANDS: Uahuka (ANSP); 7 dredge hauls, 25-45 fms., Nukuhiva; 6 dredge hauls, 22-51 fms., Ua Pou; 6 dredge hauls, 30-46 fms., Tahuata; 3 dredge hauls, 42-45 fms. Fatuhiva (all USNM). HAWAIIAN ISLANDS: Ewa Beach, Oahu (Colln. T. H. Richert); Waikiki, Oahu (USNM, Colln. T. H. Richert); Kailua Bay, Oahu (MCZ, Colln. C. S. Weaver); Makua, Oahu, in 40 ft. (DMNH); Barbers Point, Oahu (BPBM, Colln. C. S. Weaver); Keeki Nahou, Oahu (BPBM, USNM, Colln. C. S. Weaver); Honolulu Harbor, Oahu; Kahana, Oahu; Lanai (all USNM); off Kihai, Maui (Weaver, 1963). JOHNSTON ISLAND: Sand Island (USNM).

Fossil Records—INDONESIA: S Bantam, Java; age: Pliocene (Oostingh, 1938); near Kroe, Benkoelen, S Sumatra; age: Upper Miocene (Zwierzycki, 1915, p. 105).

Harpa davidis Röding, 1798

(Pl. 187, figs. 4-6)

Range—Maldives, Ceylon and eastern India to Burma, Thailand, and northwestern Sumatra.

Remarks—This species, which appears to be restricted to the coasts surrounding the Bay of Bengal, has hitherto been confused and synonymized with *Harpa major* Lamarck and *articularis* Lamarck (Habe, 1964, p. 105, pl. 33, fig. 24). I question all records of this species purporting to be from the islands in the western Indian Ocean, such as Mauritius, and from the eastern part of Indonesia.

The most useful character to differentiate it from *Harpa major* and *articularis* is the form of the brown splotch on the parietal wall which in *davidis* has the upper larger portion bisected, or almost so, by a wedge-shaped clear area which may be prolonged into the aperture by a narrow dividing band. The lower portion of the parietal blotch is bisected resulting in an isolated brown or chestnut spot at the base of the columella.

In general shape and size *H. major* and *davidis*

are similar, but the body whorl of the latter is more broadly ovate and rounded, the ribs tend to be narrower and more distant, and usually have a series of single dark chestnut lines on the ribs. Juvenile specimens usually show fine but strong spiral cords of varying width; the names *H. cancellata* Röding and *H. striata* Lamarck are based on such specimens.

Habitat—Found crawling in the sand, just underneath the surface, in shallow water at Trincomalee, Ceylon. Also trawled in deeper water off the Indian coast (Crichton, 1941, p. 330).

Description—Shell of moderate size, 47.5 to 90 mm. (1½ to 3½ inches) in length, broadly ovate with rather short, broadly conical spire. Protoconch elevated-mamillate, pale pink, of 3¼ to 3½ convex whorls. Early postnuclear whorls reticulated by axial riblets and spiral cords, moderately angulate at the shoulder; penultimate whorl and early part of antepenultimate whorl covered by extensions of earlier parietal calluses. Body whorl broadly inflated, with 10 to 12 axial ribs which are spinosely angulate at the shoulder below the sub-sutural shelf, and are generally narrower than in *H. major*; the ribs have areas of different shades of red brown or pale pink resulting from the spiral bands of the color pattern of the shell, and in addition generally dark chestnut lines that are single or closely double. Base color usually grayish pink and occasionally darker, showing a banded arrangement, and marked by axial sharply arcuate or sagittate streaks of red brown, most prominent in the area adapertural of the ribs. Aperture broadly semilunate, inner lip very gently concave or almost straight, outer lip arcuately concave, parietal and columellar callus large, marked by large upper and middle blotches separated by a triangular area; a small basal blotch is present in the center of the callus covering the lower half of the columellar area; the anterior siphon is rather broad.

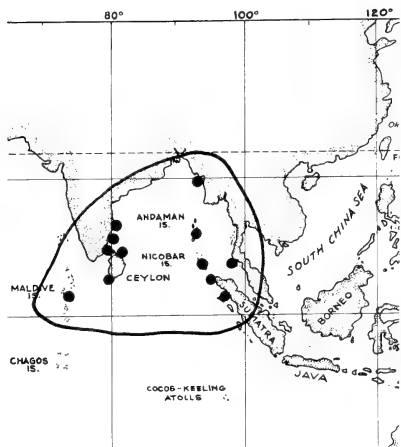
Measurements (mm.)—

length	width	no. whorls
90.3	65.7	6 large; Ceylon
83.6	59.1	5½ large; N. Sumatra
63.4	43.8	5 average; Ceylon
55.4	39.1	5½ average; Ceylon
47.5	31.1	6½ small; Andamans

Synonymy—

1798 *Harpa davidis* Röding, Museum Boltenianum, pt. 2, p. 150, no. 1878; refers to Martini, Conchyl.-Cab., vol. 3, pl. 119, f. 1092 (Coromandel).

1798 *Harpa cancellata* Röding, loc. cit., p. 150, no. 1879; refers to Chemnitz, Conchyl.-Cab., vol. 10, pl. 152, f. 1453 (Tranquebar); 1857, Küster, Conchyl.-Cab., (ed. 2), vol. 3, pt. 1B, p. 96, pl. 70, f. 4, 5.

Plate 216. Geographical distribution of *Harpa davidis* Röding.

- 1807 *Harpalis davidis* Link, Besch. Nat.-Samml. Univ. Rostock, pt. 3, p. 114.
 1816 *Harpa striata* Lamarck, Liste in Tabl. Encycl. Meth., pt. 23, Moll. et Polypes Div., p. 3; refers to pl. 404, f. 4; 1822, Lamarck, Hist. Nat. An. s. Vert., vol. 7, p. 257 (no locality); 1883, Tryon, Man. Conch., vol. 5, p. 99, pl. 41, f. 74-75.
 1852 *Harpa nablum* Mart., Mörch, Cat. Conch. Yoldi, pt. 1, p. 125 (no locality); 1860, Sowerby, Thes. Conch., vol. 3, p. 170 (in part), pl. 232, f. 15-16, pl. 233, f. 24; 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, p. 107.
 1857 *Harpa articularis* var. C. Küster, Conchyl.-Cab., ed. 2, vol. 3, pt. 1B, p. 87, pl. 70, f. 2.
 1942 *Harpa conoidalis* Lam., Gravely, Bull. Madras Govt. Museum, N. S., Nat. Hist. Section., vol. 5, no. 2, p. 67, f. 12h; 1952, Satyamurti, op. cit., vol. 1, no. 2, pt. 6, p. 196, pl. 19, f. 1a, 1b. (not *conoidalis* Lam., 1822)

Types—Röding's name is based on a figure and description given by Martini (cited above), based in turn on specimens in his collection, the present location of which is unknown. Martini gives Coromandel as the provenance of his specimens; we further restrict the type locality to Madras, India. Similarly the specimen upon which *H. cancellata* Röding is based was not found in the collection of Zoological Museum in Copenhagen. The type of Lamarck's *H. striata* cannot be found in the Muséum d'Histoire Naturelle in Geneva.

Nomenclature—This species has been misunderstood by most authors and misidentified or synonymized with other species. I can find in Reeve's monograph (Reeve, 1843) no figures that with certainty can be identified with this species; unfortunately one cannot determine from most of his descriptions and figures the nature of the colu-

mellar blotches. Tryon, in 1883, placed this species under *conoidalis* Lamarck. Sutor in the most perceptive study of the group to date (Sutor, 1877) describes as a distinct species *Harpa nablum* Martini, under which he cites the Martini figure which is the figure on which Röding based his *davidis*. Workers on the Indian fauna have usually used the name *H. conoidalis* Lam. (= *major* Röding) for this species. The shells that Habe (1961, p. 68, pl. 33, fig. 24. and 1964, p. 105, pl. 33, fig. 24) illustrates under *H. davidis* are not that species, being in one case (1961) *H. major* Röding, and in the other (1964) *H. articularis* Lamarck.

Records—MALDIVES: (BMNH). CEYLON: Galle (AMNH); Elisabeth Pt. Trincomalee; Kacheri to Powder Bay, Trincomalee (both ANSP). INDIA: Rameshwaram, Pamban Id., Madras (USNM); Tranquebar (ZMC); Madras (BMNH, MCZ, USNM, ZMC). ANDAMANS (ZMC). NICOBAR IDS.: (ZMC). BURMA: 17 mi. SE of Akyab (ANSP). THAILAND: Ko Phuket (ANSP). INDONESIA: Sumatra, NW Atjeh; nr. Kutaradja, Atjeh; Tapatoean, Atjeh (all RNHL).

Harpa articularis Lamarck, 1822

(Pl. 188, figs. 5-7; Pl. 217)

Range—Philippines and Indonesia to Western Australia, Queensland, and Fiji.

Remarks—This easily recognized species is characterized by its broadly ovate shape, relatively narrow ribs strongly marked with dark chestnut lines, and particularly by the large chestnut ventral splotch which covers the whole thin parietal and columellar calluses, with the slender ribs on the ventral side showing through the splotch. The overall pattern of markings between the ribs is more subdued and semi-obscure than in the other species.

The geographical range of this species is rather restricted, as a glance at the distributional map shows. It also appears to have a geological history, as a specimen figured as *Harpa conoidalis* Lamarck ? by Martin (1879-80, p. 41, pl. 8, fig. 1) is so close in appearance to *Harpa articularis* that I am assigning it here.

Description—Adult shell 41 to 96 mm. (1½ to 3¾ inches) in length, broadly ovate, usually rather thin, last whorl large, broadly ovate, spire broadly conical. Nuclear whorls conical, ¾ in number, rounded, smooth, flesh-colored or darker. Early postnuclear whorls with two or three spiral cords and many strong lamellose axial ribs that are made strongly and angularly denticulate at the shoulder, accentuated by the presence of a shallow groove just below the shoulder of the whorls. The antepenultimate whorl has the lower half

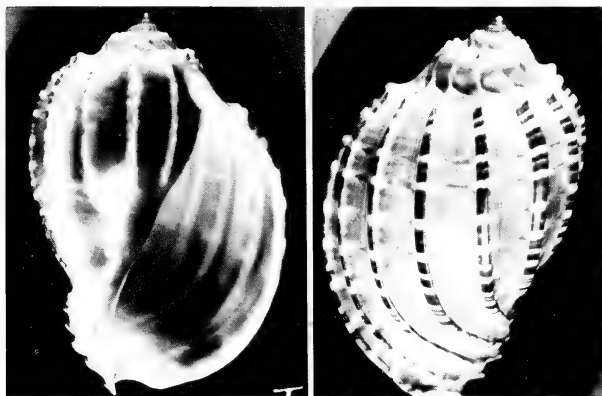


Plate 217. *Harpa articularis* Lamarck, 1816. Holotype. Muséum d'Histoire Naturelle, Genève. 70 mm.

covered by a glaze, while the penultimate whorl is wholly covered by the glaze formed by the extension of former parietal calluses. Last whorl of larger specimens with 12 to 16, usually rather narrow ribs, strongly marked by dark chestnut lines that are usually in groups. Color of shell varies from pinkish or brownish flesh-colored to reddish grayish brown, with a more or less obscure pattern of spiral bands of white and axial, zigzag, darker lines with high sharp peaks where they cross the white bands, forming there a series of sagittate markings. Aperture oval, posteriorly acuminate, outer lip evenly rounded, ventral surface of body whorl covered by an uninterrupted chestnut colored parietal glaze, with only the axial ribs showing through; callus at posterior junction of outer lip white. Interior of outer lip is pale below the junction with the body whorl and in the anterior canal area.

The animal of a specimen from Virac, Catanduanes, Philippines, is paler in color than that of *H. major*, distantly spotted with reddish brown and the anterior edge of the propodium is gently undulate.

Measurements (mm.)—

length	width	no. whorls	
95.6	63.8	6%	large; Philippines
92.6	60.4	6%	large; Adele Id., W Australia
74.2	51.4	6%	average; Tin Can Bay, Queensland
67.8	45.0	7%	average; Catanduanes, Philippines
49.6	32.2	5%	small; Philippines
40.9	27.1	5%	small; Tambisan, North Borneo

Synonymy—

- 1811 *Harpa delicata* Perry, Conchology, pl. 40, fig. 2 [*nomen oblitum*]
 1816 *Harpa nobilis* Lamarck, Liste, Tabl. Encycl. Method., pt. 23, Moll. et Polypes Divers, p. 3; refers to Encycl. Method, Moll. Test., pl. 404, fig. 3a, b (no locality). Not *Harpa nobilis* Röding, 1798.
 1822 *Harpa articularis* Lamarck, Hist. Nat. Anim. sans Vert., vol. 7, p. 256 (no locality); 1835, Kiener, Spec. Gen. Icon. Coq. Viv., vol. 8, Genre Harpe, p. 8, pl. 2, fig. 3; 1843, Reeve, Conch. Icon., vol. 1, *Harpa*, pl. 2, fig. 4a-d; 1857, Küster, Neues Syst. Conch.-Cab., ed. 2, vol. 3, pt. 1, p. 87, pl. 66, figs. 3-5; 1877, Sutor, Jahrb. deutsch. Malak. Ges., vol. 4, p. 102, pl. 5, fig. 3.
 1964 *Harpa davidis* Röding, Habe, Shells of the Western Pacific in Color, vol. 2, p. 105, pl. 33, fig. 23. Not *H. davidis* Röding, 1798.
 1966 *Harpa davidis* Röding, Habe and Kosuge, Shells of the World in Colour, vol. 2, p. 79, pl. 30, fig. 1. Not *H. davidis* Röding, 1798.

Types—I found two specimens labeled *articularis* in the collections of the Muséum d'Histoire naturelle de Genève, of which I have chosen as lectotype the specimen illustrated in Plate 217.

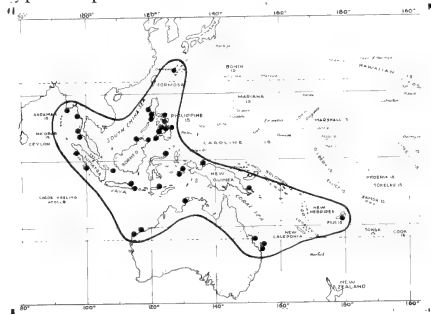


Plate 218. Geographical distribution of *Harpa articularis* Lamarck.

Records—JAPAN: Okinawa, Ryukyus (ANSP). PHILIPPINES: Iba, Zambales, Luzon; Mariveles, Bataan, Luzon; Corregidor Id., Luzon; Calatagan, Batangas, Luzon (all ANSP); Ternata, Cavite, Luzon (USNM); Lubang Id., Mindoro (ANSP, MCZ, USNM); Calapan, Mindoro (AMNH, ANSP, MCZ); Puerto Galera, Mindoro (AMNH, MCZ); Virac, Catanduanes (USNM); Ticao (AMNH); Maqueda Bay, Samar (MCZ); Capul Id., NW Samar (ANSP); Cebu City, Cebu (ANSP, USNM); Dumaguete, Negros; W of Bucas Grande Id., Siargao, Mindanao (both USNM); Mambajao, Camiguin Id., Mindanao (ANSP); Zamboanga, Mindanao (DMNH). BURMA: 50 mi. SW of mouth Irawaddy River, Preparis N. Channel, 53 m.; 57 mi. NW of Tavoy Id., 39 m. (both ANSP). THAILAND: Andaman Sea, 55 mi. W of Ranong, 73 m.; South end Pa Tong Bay, Ko Phuket (both ANSP). MALAYSIA: off Tambisean, North Borneo (USNM); Sapi Id., nr. Jesselton, North Borneo (ANSP). INDONESIA: Tapaktuan, Ateih, NW Sumatra, Padang, Sumatra; Belitung; Madura (all RNHL); Bali (MCZ); Larantuka, Flores; Ceram; Ambon; Manado, Celebes (all RNHL); Semberbata, Japen Id., Geelvink Baai, W Irian (ANSP). PAPUA-NEW GUINEA: Goodenough Id. (AMNH). WESTERN AUSTRALIA: Exmouth Gulf, Adele Id.; Legendre and Delambre Ids., Dampier Archipelago (all WAM). NORTHERN TERRITORY: near Darwin (ANSP). QUEENSLAND: Keppel Bay, 20 fms. (AMS); Tin Can Id. (USNM); off Tin Can Bay, SE of Fraser Id., 30-35 fms. (AMS, DMNH, WAM, NMV); E of Fraser Id. in 30 fms. (DMNH). FIJI: Ngau Id. (BM).

Fossil Records—INDONESIA: north of Sindangaran, S coast of western Java; age: Upper Miocene: Tjilangang beds (Martin, 1879-80, p. 41).

Harpa ventricosa Lamarck, 1816

(Pl. 188, figs. 1, 2; Pl. 219)

Range—Red Sea and East Africa to Seychelles and Mauritius.

Remarks—This species occurs in the western part of the Indian Ocean. References to its occur-

rence in India, Indonesia, and the Philippines are to be regarded as doubtful, and are based on old specimens in museum collections (see under "Records"), or based on the use of this name for what is now known as *H. major* Röding.

Compared to its closest relative, *Harpa major* Röding, *H. ventricosa* is characterized by the squarish aspect of the body whorl when viewed from the apertural side, the flattened side and angulate shoulder where the ribs are more erect and bear a strong triangular spine with less conspicuous spines below the shoulder. The chestnut intercostal painting is more regularly, deeply, and multiplicately arcuate; the chestnut markings on the parietal wall are decidedly less extensive.

Habitat—In 0 to 15 feet, on sandy bottom; in one locality on the southwest coast of Nosy Bé, Madagascar, it is recorded as living in the marine "grass" *Cymodocea*.

Description—Shell 48 to 110 mm. (1½ to 4½ inches) in length, broadly oval, with left side rather flattened when viewed from apertural side, solid, body whorl large. Spire conical; protoconch elevated-conical, flesh-pink, 4½ whorls, smooth; earliest portion of first postnuclear whorl without spiral cords and with several distant prosocline, shallow-sigmoidal riblets, succeeding portions angulated by several spiral cords that cross the riblets, which become increasingly lamellar; the ribs at the uppermost, subsutural cord form a conspicuous projection. The lower portion

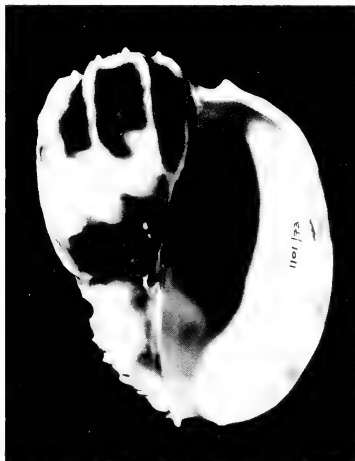


Plate 219. Two views of the holotype of *Harpa ventricosa* Lamarck, 1816. This specimen was illustrated in the Encyclo-

pédie Méthodique, vol. 3, pl. 404, figs. 1a, 1b. Photo by G. Dajoz, courtesy of Muséum d'Histoire Naturelle Genève.

Jubal (ANSP). ADEN (BM). SOCOTRA: north coast (ANSP). MADAGASCAR: between Ambotoloaka and Madiorankely, SW of Nossy Bé; Amforah, Nossy Be (both ANSP); S of Ambombohé (AMNH); Nossy Faly (FNHL). ÎLE GLORIEUSE: (USNM). SEYCHELLES: (MCZ); Mahe (BM). MAURITIUS: (AMNH, ANSP, BM, DMNH, MCZ, USNM); Mahebourg (USNM); Ile Flaman (DMNH).

Doubtful Records—Tranquebar Coast, India (RNHL); Madura (RNHL) and Ambon, Indonesia (MCZ, RNHL); these three records are based on specimens from old collections, and should be regarded as doubtful. No specimens of this species have been found in India or Indonesia in recent years. Two specimens in the USNM are labeled as coming from Luzon and from Negros Oriental; the localities of these specimens, obtained from a dealer and from an amateur collector respectively, are suspect.

Harpa costata (Linne', 1758)

(Pl. 187, figs. 1-3; Pls. 221-223)

Range—Islands of the western Indian Ocean: Mauritius, Rodrigues, and northeastern Madagascar.

Remarks—This is one of the most distinctive species, characterized by its broad shape, the large number of crowded ribs, which are rather sharply pointed at the shoulder-angle of the body whorl forming a broad subsutural channel; its distinctive coloration consists of numerous spiral bands of varying shades of flesh color and white.

Habitat—On sand banks, frequently in shallow water—10 inches to 6 feet.

Description—Shell 70 to 100 mm. (2½ to 4 inches) in length, broadly subquadrate, solid, last whorl very large. Spire broadly conical; protoconch elevated-conical, flesh pink, whorls 4½, smooth; early postnuclear whorls broadly shouldered, with spaced axial riblets and fine spiral cords below the shoulder and light chestnut spots on the shoulder between the protractively curved riblets. On the later postnuclear whorls the axial riblets become more crowded, and on the shoulder become increasingly lamellar towards the upper portion where they are adnate to the preceding whorls, fusing and covering the lower half of the exposed whorls; in the last half of the penultimate whorl the spiral cords become obscure, in some specimens completely covered by the fused upper part of the ribs of the following whorl. On the body whorl the ribs are crowded, shiny, 30 to 40 and more in number, depending on the size of the shell; they are lamellar, recurved, with a triangular, spine-like projection at the shoulder angle, forming a broad, subsutural channel; often more or less flattened in the last half of the body whorl, and fused above the conspicuous siphonal fasciole over which the lamellar

ribs are strongly continued. Between the ribs are fine axial cords crossed by distant, subobscure spiral cords. External color of shell pale flesh color, with bands of varying darker shades and white; occasional subquadrate spots of chestnut color are present between the ribs, usually in an irregular peripheral band. Aperture broad, appearing subrectangular because of the broad subsutural shelf; inner lip almost straight, outer lip angled at the shoulder and rather effuse at the base, slightly thickened within; parietal callus rather thin, columellar callus heavier, both usually somewhat suffused with yellow, and with three chestnut blotches, the upper and middle ones moderately large, generally subequal, the lower one on the columellar callus small, obscure or absent; interior of aperture often with a yellow wash, especially near the base.

From color slides kindly sent me by Mrs. E. Coucaud of Port Louis, Mauritius, (Plate 221) the foot of *H. costata* appears to be relatively broader than in either *ventricosa* or *major*, and the posterior end is rather obtuse with a keel marking the posterior part of the foot.



Plate 221. Dorsal view of *Harpa costata* (Linne') from Mauritius (photo by Mrs. E. Coucaud).

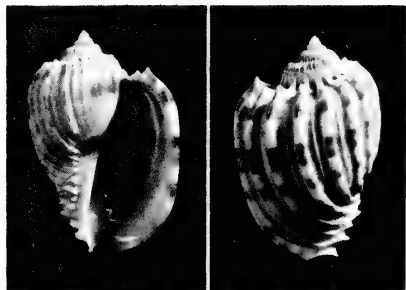


Plate 222. *Harpa costata* (Linné) Holotype of *Harpa costata* var. *laetifica* Melvill, 1916. National Museum Wales. 42.1 mm. in length.

Measurements (mm.)—

length	width	no. whorls
99.0	78.0	large; Mauritius
97.4	69.4	large; Ile aux Fouquets, Mauritius
92.0	67.2	6%; average; Le Morne, Mauritius
85.1	61.0	average; Ile aux Fouquets, Mauritius
81.8	63.9	average; Ile aux Fouquets, Mauritius
71.3	54.8	6%; small; Mauritius

Synonymy—

- 1758 *Buccinum costatum* Linné, *Systema Naturae*, ed. 10, vol. 1, p. 738 (no locality); type locality here designated: Mauritius;
- [1785 *Harpa imperialis* Chemnitz, *Conchylien-Cabinet*, vol. 10, p. 184, pl. 152, fig. 1452 (no locality); non-binominal.]
- 1822 *Harpa imperialis* Lamarck, *Hist. Anim. sans Vert.*, vol. 7, p. 225 (Mers de l'Amerique meridionale?); 1853, *Chenu, Illustr. Conchyliologiques*, vol. 4, pt. 85, *Harpa*, pl. 1, fig. 1, 1a, 1b.
- 1822 *Harpa multicostata* Sowerby, *Genera of Shells*, no. 3, *Harpa*, fig. 1 (Indian Ocean).
- 1835 *Harpa ventricosa* var. *Kiener*, *Coquilles Vivantes*, vol. 8, *Genre Harpe*, p. 7, pl. 2, fig. 2 (no locality).
- 1843 *Harpa imperialis* Chemn., Reeve, *Conchologia Iconica*, vol. 1, *Harpa*, pl. 2, fig. 5; 1857, Küster, *Neues Syst. Conchylien-Cabinet*, ed. 2, vol. 3, pt. 1B, p. 86, pl. 66, figs. 1-2, pl. 70, fig. 1.
- 1860 *Harpa costata* Linné, Sowerby, *Thesaurus Conchologica*, vol. 3, p. 169, pl. 231, figs. 4-5, pl. 233, fig. 23 (young); 1863, Tryon, *Man. of Conch.*, vol. 5, p. 97, pl. 40, fig. 58.
- 1877 *Harpa costata* var. *gruneri* 'Maltzan' Sutor, *Jahrb. deutsch. Malak. Gesellschaft*, vol. 4, p. 102, pl. 4, fig. 2 (no locality).
- 1916 *Harpa costata* var. *laetifica* Melvill, *Journ. of Conch.*, vol. 15, p. 31 (no locality).

Types—There is no specimen of this species in the Linnean Collection in London, and Linnaeus did not cite any reference in his original description. According to Odhner (unpublished list and microfilm) a specimen is present in the Museum Ludovicae Ulricae, and this specimen I hereby designate as lectotype. The type locality I am designating as Mauritius. The specimen upon which Chemnitz based his description and figure of his *Harpa imperialis* and which he stated came "Ex Museo Spengleriano" is present in the Zoological Museum in Copenhagen with a label in Spengler's handwriting. This specimen I am designating as the lectotype of Lamarck's species *imperialis*; there are no specimens of *H. imperialis* in the Lamarck collection in Geneva. The type of *gruneri* Sutor was in the Maltzan collection which according to Dance (1966, p. 293) was purchased by a dealer and dispersed; its present location is unknown. The holotype of Melvill's variety *laetifica* is in the Melvill-Tomlin Collection in the National Museum of Wales in Cardiff (Plate 222).

Records—MAURITIUS: Le Morne, SW coast (DMNH, USNM); off Ile Marianne and Ile aux Fouquets, W coast (ANSP, Colln. W. N. Carpenter); Mahebourg (ANSP, DMNH); Les Bénéitiers, W coast (AMNH). RODRIGUES (BM), MADAGASCAR: 28 km. S of Antalaha, NE coast, in 2 meters (Mme. H. Bouchard, in litt.).

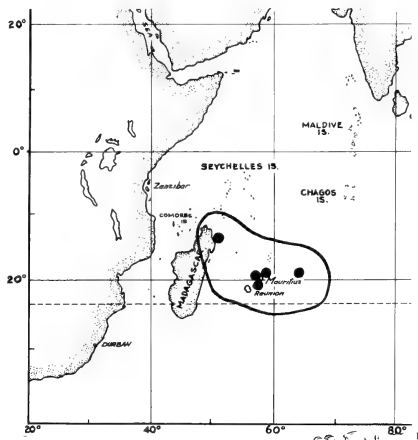


Plate 223. Geographical distribution of *Harpa costata* (Linné).

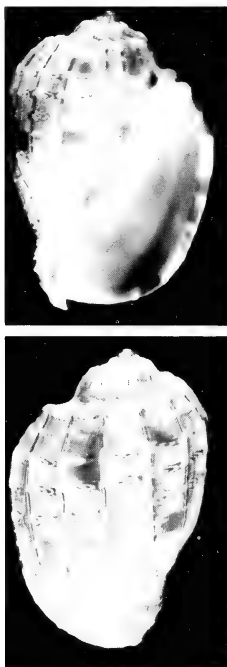
Harpa doris Röding, 1798

(Pl. 189, figs. 12-16; Pl. 224)

Range—From the Cape Verde Islands to Luanda, Angola; Ascension Island.

Remarks—*Harpa doris* is most closely related to the only other species found outside of the Indo-Pacific region, namely *Harpa crenata* Swainson of the Panamic province. This relationship is demonstrated by the presence in both species of vivid, spirally oriented, narrow bands of color markings, often in a more or less sagittate pattern, as well as blotches of solid color; in fresh specimens of both species the ribs are marked on their abapertural side by a fine, interrupted chestnut line. *Harpa doris*, differs from *crenata* in being smaller, somewhat more slender, the ribs with a greater tendency to becoming broad, and by the spirally oriented series of blotches being rose or rose-orange rather than chestnut.

Description—Shell 77 to 31 mm. (3 to 1¼ inches)



in length, usually elongately oval and rather thin, but occasionally broader and solid. Spire broadly conical; protoconch elevated-mamillate, 3¼ whorls, pale pink or flesh-color, smooth; first 1½ postnuclear whorls with low, sharp axial ribs crossing distant rounded spiral ridges; between the ribs the spiral sculpture is crossed by crowded microscopic axial threads. On subsequent whorls the ribs show a spinose angulation at the shoulder, and the spiral sculpture becomes increasingly obscure, first on the subsutural ramp above the shoulder, and then on the remainder of the whorl. Body whorl elongate ovate, with a distinct subsutural shelf above the shoulder angulation which is marked by the strong triangular spines of the ribs; ribs 11 to 13, occasionally 14, in number, generally slender and rather low, and triangular in cross-section; occasionally those towards the aperture are greatly broadened; ribs marked by a thin brown interrupted line on the crest. In the stout broad form, all the ribs on the body whorl are rather broad and heavy and rather angulate at the periphery. Base color pale flesh-pink, occasionally darker, with the early postnuclear whorls orange-pink to purplish pink; bands of this color are present on the body whorl below the angulation at the shoulder, in the middle of the whorl, and above the base, the latter narrower than the other two; these bands often are bicolorous with alternate squarish blotches of the orange shade and the purplish pink shade; narrow, subequally spaced bands of chestnut marked by sagittate white spots mark the body whorl, these bands occasionally linked by obscure, chestnut, arcuate lines. A thin glaze covers the parietal and columellar areas which are marked by three separated brown spots: one just above the juncture of the

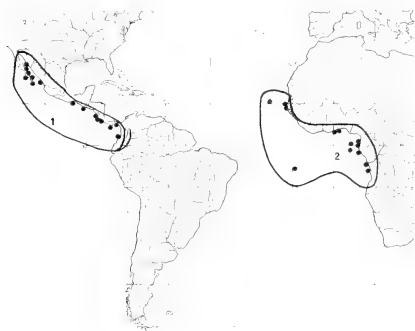


Plate 224. *Harpa doris* Röding. Holotype of *Harpa rosea* Lamarck, 1816. Muséum d'Histoire Naturelle (Genève). 55 mm. in length.

Plate 225. Geographical distribution of: 1, *Harpa crenata* Swainson, 2, *Harpa doris* Röding.

outer lip with the body whorl, another, the largest, just above where the columella joins the parietal wall, and the third on the expanded columellar lip; the last two spots are separated by the covered siphonal fasciole. Aperture elongate-ovate, semi-lunate, the outer lip gently arcuate.

Measurements (mm.)—

length	width	no. whorls	
77.2	49.8	6%	large; Senegal
49.7	29.0	7%	medium; Cape Verde Ids.
48.1	29.5		medium; Cape Verde Ids.
40.1	25.2		small; Annobón
31.1	20.6		small; Fernando Poo

Synonymy—

- [1786 *Buccinum pandura* 'Solander' Lightfoot, Portland Catalogue, pp. 17, 103 (Guinea), *nomen nudum*].
 1798 *Harpa doris* Röding, Museum Boltianum, p. 150; refers to Martin, Conchylien-Cabinet, vol. 3, p. 419, pl. 119, fig. 1094 (no locality given; type locality here designated: Accra, Ghana); 1948, M. Smith, Triton Helmet and Harp Shells, p. 47, pl. 16, fig. 4.
 1807 *Harpalis doris* Link, Beschreibung Naturalien Sammlung Univ. Rostock, pt. 3, p. 114.
 1816 *Harpa rosea* Lamarck, Encyclopédie Méthodique, vol. 3, pl. 404, fig. 2; Liste, p. 3; 1822, Lamarck Hist. Nat. Anim. sans Vert., vol. 7, p. 257; 1843, Reeve, Conchologia Iconica, vol. 1, *Harpa*, pl. 4, figs. 8a, b, c, d; 1950, Nicklès, Mollusques Testacés Marins Côte Occid. d'Afrique, p. 113, fig. 204.

Types—Röding based the species *doris* on a description and figure published by Martini, based in turn on a shell in the latter's collection. This specimen must be presumed to be lost. The type of *H. rosea* Lamarck is in the Lamarck Collection in the Museum of Natural History in Geneva.

Records—CAPE VERDE ISLANDS: (AMNH, BM, DMNH, MCZ). SENEGAL: (AMNH, BM, DMNH, RNHL). GAMBIA: (AMNH). GHANA: (BM); Accra (AMNH); Takoradi; Elmina (both Buchanan, 1954). SPANISH EQUATORIAL AFRICA: Santa Isabel, Fernando Poo (USNM); Corisco, Rio Muni (AMNH); Annobón (USNM). SAO TOME: (Knudsen, 1956). GABON: Omboue (= Namino, Ferman-Vaz, (Nicklès, 1952); ANGOLA: Santa Antonio de Zaire (Tomlin and Slackford, 1914); Luanda (MCZ). ASCENSION ISLAND: (DMNH, MCZ); English Harbour (Colln. K. Jourdan); Georgetown Beach, (DMNH).

The form generally found washed up on the beaches of Ascension Island is a broader, heavier shell, with broader ribs that are more or less angulate at the periphery (Pl. 189, figs. 15, 16). I have seen two specimens from Santa Isabel on Fernando Poo that also belong to this form. For a time I considered this stout form to be a distinct subspecies restricted to the islands off the African coast. However, I have recently seen a fresh specimen of the normal form washed up on the sandy beach at English Harbour on Ascension Island. This is one of the few localities on the island where a sandy substrate is present. It is likely therefore

that the normal form occurs where a sand bottom is found, and that in a rocky area where the bottom consists of rocks or cobbles, as in most of Ascension Island and on Fernando Poo, the species develops a heavier shell. The two forms can thus be considered ecophenotypes of the species *Harpa doris* Röding.

Harpa brochoni 'Benoist' Cossmann, 1899

(Pl. 226)

Range—Late Lower Miocene of France (Burdigalian).

Remarks—This species is a typical *Harpa*, as evidenced by the strong development of the parietal callus over the ventral surface of the body whorl and over the lower part of the penultimate whorl. Its closest relative is the West African *Harpa rosea* Röding, some of whose beachworm specimens closely resemble *H. brochoni*. The aperture of the latter is shorter, however, with the base less patulous, and the knobbing at the shoulder angle is heavier.

Description—(translated from Peyrot, 1928)—Shell thick. Size rather large. Form ventricose; spire short, composed of five to six whorls, the first smooth, constituting the protoconch which is badly preserved on my specimens; the following whorls, first convex, then angulate, are ornamented with a dozen narrow axial ribs, widely separated, subspinose on the angle; from the penultimate whorl they cross the suture and join each other on the preceding whorl; last whorl very large, ventricose, the ribs on it becoming heavy and lamellose; they cross posteriorly the sutural ramp extending onto the preceding whorl while joining each other; anteriorly they curve backwards hook-shaped over the siphonal fasciole, which thus appears strongly lamellose; the intercostal spaces show feeble separated spiral striae.



Plate 226. *Harpa brochoni* 'Benoist' Cossmann, 1899. Lower Miocene of France. 55 mm. (from Peyrot, 1928 pl. 11, figs. 30-32).

Aperture very dilated, above all anteriorly where it is strongly sinuate; outer lip rectilinear, slightly oblique, with a weak sinus at its junction with the suture, externally thickened by the last rib; internally smooth; columellar margin extensively spread over the ventral surface of the last whorl where it is rather thin, becoming thicker anteriorly where it forms a slight swelling on the edge of the siphonal fasciole, in the columellar area, before terminating in a point on the siphonal notch. Dimensions: height, 55 mm.; max. diam. 34 mm.

Synonymy—

[1884 *Harpa brochoni* Benoist, Procès-Verbaux Soc. Linn. Bordeaux, 1884, p. LXVII, nom. nud.]

1899 *Harpa brochoni* Benoist, Cossmann, Essais, paléoconch. comp., livr. 3, pp. 74, 75, pl. 4, fig. 3 (near Bordeaux, France).

1928 *Harpa brochoni* Benoist, Peyrot, Conch. Négative Aquitaine, vol. 5, p. 369, pl. 11, figs. 30-32 (Saucats, S of Bordeaux).

Harpa josephinae Sacco, 1890

(Pl. 227)

Range—Middle Miocene of northern Italy (Helvetian).

Remarks—This small species (19 mm. in length) is compared by the author with *Harpa ventricosa* Lamarck but it is more slender, not as broad as either *ventricosa* Lamarck or *major* Röding. In fact it resembles more closely *Harpa doris* Röding of West Africa, but the ribs are more numerous and are not as spinose below the subsutural ramp, and the body whorl does not show the angulation below the spinose shoulder of that species. The lack of the expanded parietal callus typical of *Harpa* may be due to the possible juvenile condition of the unique holotype.

Description (freely translated from the original)—The following comments distinguish this species from *H. bellardii*:

Shell smaller, very slightly more ovate. Ribs stouter (especially at the base), less elevated, occasionally less numerous; near the suture slightly flattened, above the base generally more widely

separated. Transverse striae nearly obsolete above, below very few, occasionally crossing the ribs. Aperture slightly wider, especially below. Siphon a little broader. Height 19 mm., width 12 mm.

Synonymy—

1890 *Harpa josephinae* Sacco, Moll. Terr. Terz. Piemonte e Liguria, pt. 7, p. 9, pl. 1, fig. 2a, b (Helvetian of hills near Turin).

Harpa americana Pilsbry, 1922

(Pl. 228)

Range—Middle Miocene of the Dominican Republic and southern Vera Cruz, Mexico.

Remarks—This species is, as Pilsbry states, close to *Harpa doris* Röding of the West African fauna, differing in the aperture being narrower anteriorly and in possessing conspicuous fine spiral striation between the ribs; the spiral striation in *doris* is visible only in certain specimens and even then is rather obscure. *H. americana* agrees rather closely with *H. josephinae* Sacco of the Miocene of northern Italy, although the spiral striation is more pronounced in the American species, and the ribs are more spinose at the shoulder.

Through the kindness of Dr. Horace C. Richards I have been able to examine the holotype of *Harpa americana*. As the figure given by Pilsbry agrees in all particulars with the type, and as it clearly shows the essential characters I have reproduced this illustration rather than give a photograph of the type.

The characters of the nuclear whorls are not described by Pilsbry nor shown clearly in his figure. The protoconch is erect-mamillate with the first whorl lost; the first 1½ of the remaining

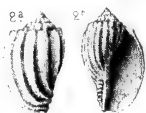


Plate 227. *Harpa josephinae* Sacco, 1890. Miocene of northern Italy. 19 mm. (from Sacco, 1890, pt. 1, figs. 2a, 2b).



Plate 228. *Harpa americana* Pilsbry, 1922. Middle Miocene of Dominican Republic. 33.3 mm. (from Pilsbry, 1922, pl. 23, fig. 13).

whorls shows the basal keel just at the suture that is typical of the protoconch of the genus *Harpa*.

The measurement of the width of the type given by Pilsbry is in error; the true figure is given below following the description.

Perrilliat (1960, p. 24) describes and figures a slightly larger specimen collected in southern Vera Cruz, 11 kilometers east of Coatzacoalcas; this and another specimen mentioned by her, measure respectively 41 and 37 mm. in height. A smaller shell from the same locality, 26.0 mm. high, is in the collections of the U.S. Geological Survey.

Description (copied from Pilsbry)—The shell is ovate, of about 6 whorls, of which three smooth ones form the nipple-shaped embryonic shell, the last whorl of which, together with part of the first sculptured whorl, are very narrow. The last whorl has about eleven low and narrow axial ribs which rise into small spines where they pass over the angle bounding a narrow flattening below the suture. The whole surface below this angle is spirally striate, the striation strongest in the concavity of the sides below. The aperture is narrow for this genus. A thin callus spreads forward over the ventral convexity.

Length 33.3 mm., width 19.4, Dominican Republic. Holotype, ANSP 4061; length 26.0 mm., width 16.3 mm., Coatzacoalcas-Villa Hermosa Highway, Vera Cruz, Mexico, USGS Colln.

Synonymy—

- 1877 *Harpa rosea* Lam., Gabb, Trans. American Phil. Society, vol. 15, p. 214. Not *H. rosea* Lamarck, 1816.
1922 *Harpa americana* Pilsbry, Proc. Acad. Nat. Sci. Philadelphia, 1921, p. 337, pl. 23, fig. 13; 1960, Perrilliat, Paleontologia Mexicana No. 8, p. 24, pl. 3, figs. 18, 19.

Harpa crenata Swainson, 1822

(Pl. 189, figs. 1, 2; Pl. 225)

Range—Magdalena Bay, Baja California and southern part of Gulf of California, Mexico, to Gorgona Island, Colombia.

Remarks—This species is most closely related to *Harpa doris* Röding of the West African marine province. These two species are the only living representatives of a small species complex that had its center in the Caribbean area. The rare *Harpa americana* Pilsbry from the Miocene of the Dominican Republic and Tehuantepec, Mexico is probably close to the ancestral stock of both species. We may conjecture that this stock once inhabited the West Tethyan Sea, or spread to the

Panamic and West African areas from the Caribbean, and species became established there while the group died out in the Caribbean.

H. crenata differs from *doris* Röding in being generally larger, broader, the spire relatively lower and broader, the more slender ribs marked more consistently by a fine interrupted chestnut line, and by the squarish blotches being chestnut-brown rather than pink or orange.

The body whorl is more markedly angulate below the shoulder, the ribs bearing more numerous spines between the subsutural shoulder and the periphery.

Habitat—On clay bottom in 40-55 meters (Parker, 1964, pp. 155, 172).

Description—Shell 32 to 91.5 mm. (1¼ to 3¾ inches) in length, broadly oval, body whorl large, more or less strongly angulate at shoulder. Spire broadly conical; protoconch elevated-mamillate, pale corneous, 3½ whorls, smooth; axis of protoconch and first postnuclear whorl sometimes at a slight angle to that of rest of shell; first postnuclear whorl sculptured with distant axial riblets and two spiral cords forming a coarse reticulate pattern which becomes complicated by addition of further spiral cords; in the second postnuclear whorl the upper spiral cord marks an angulate shoulder, the ribs become more lamellar, and the upper terminus of the ribs curves forward and forms a layer adnate to lower part of preceding whorl; the ribs at the angulate shoulder are produced into a lamellar, triangular spine; occasionally the next spiral row of smaller spines is visible on the penultimate whorl covered by the thin upper edge of the former parietal callus. Body whorl large with a series of subequidistant ribs, generally narrow, triangular in cross section, but occasionally thickened, especially towards the outer lip; the upper portion of the rib marked by a series of three to four spirally aligned triangular spines, the uppermost one, below the subsutural ramp, the largest, while the third one below the suture is next in size and often marks a distinct angulosity of the body whorl; ribs marked on the crest with a narrow interrupted chestnut line; ground color between ribs pale yellowish pink or grayish yellowish pink to pinkish gray or brownish pink with a series of bands of varying width of short, axial, zigzag chestnut lines that occasionally become irregularly broadened on the adapertural side of the ribs, especially near the outer lip. Large irregularly shaped blotches of chestnut are present between the ribs on the upper portion of the body whorl. The color markings of the body whorl appear more conspicuously banded within

the aperture. Aperture ovate, moderately narrow above where there is a deep subsutural sinus and effuse below; outer lip only slightly thickened, bluntly denticulate at edge, especially in basal half; inner lip almost straight to gently concave. Parietal wall covered by a thin glaze, with a large brown-chestnut splotch at the junction of columellar and parietal lip and two splotches of varying sizes, one on parietal wall near junction of outer lip, the other between the columellar lip and the siphonal fasciole.

Measurements (mm.).—

length	width	no. whorls
92.6	63.7	7
78.9	48.8	6½
73.3	47.9	7½
64.5	39.9	medium; Gulf of California
34.0	21.7	6½ small; Gulf of California

Synonymy.—

- 1822 *Harpa crenata* Swainson, Catalogue Shell Colln. Bligh, Appendix, p. 5. (no locality given; Acapulco, Guerrero, Mexico, designated as type locality by Emerson, 1964); 1843, Reeve, Conch. Icon., vol. 1, Harpa, pl. 4, fig. 9a, b, c; 1964, Emerson, American Mus. Novitates, no. 2202, pp. 3-5, fig. 1.
- 1832 *Harpa scriba* Valenciennes, in Humboldt and Bonpland, Voyage reg. equinox. Nouv. Continent, pt. 2, Rec. Observ. zool. anat. comp., vol. 2, p. 323 (Acapulco, Mexico).
- 1834 *Harpa rivoliiana* Lesson, Illustr. de Zoologie, (12), pl. 36, fig. 1, 2 ("Japonia?"); 1860, Sowerby II, The-saurus Conch., vol. 3, p. 171, pl. 232, fig. 12, 13 (Acapulco).
- 1835 *Harpa rosea* Kiener, Spec. Gen. Icon. Coquilles Viv., vol. 8, Genre Harpe, pp. 11-12 (in part), pl. 5, fig. 8. Not *Harpa rosea* Lam.
- 1839 *Harpa rosea crenata* Gray, Zoology Capt. Beechey's Voyage, p. 122, pl. 34, fig. 5.

Types—The type of *crenata* Swainson was in Mrs. Bligh's collection which was sold at auction in May 1822. Although many of the rarities came to the British Museum with the Broderip Collection, no specimen that might be considered to be the type was found in that collection; the type must be considered to be lost. The types of *scriba* Valenciennes and *rivoliiana* Lesson are not in the Museum National d'Histoire Naturelle in Paris, and their present whereabouts are unknown.

Records—MEXICO-BAJA CALIFORNIA: Mulege Bay (USNM); Loreto; Magdalena Bay (both MCZ); La Paz (AMNH, ANSP, MCZ, RNHL); Cabo San Lucas (USNM). SONORA: Guaymas; Mazatlan (both ANSP, BM, MCZ, USNM). OAXACA: Salina Cruz (USNM). GUATEMALA: off Puerto San José (ANSP). COSTA RICA: Salinas Bay (ANSP, BM); Bahía Huevos, W of Puerto Culebra (ANSP); Golfo de Nicoya (USNM). PANAMA: Isla Coiba (Univ. Panama); Isla Pedro González, Islas Perlas (ANSP). COLOMBIA: Isla Gorgona (AMNH).

Fossil Records—PLEISTOCENE: Punta Coyote, Baja California, Mexico (Hertlein, 1957, p. 59); Rio Colotepec, Oaxaca, Mexico (Palmer and Hertlein, 1936, p. 68).

Harpa myrmia Olsson, 1931

(Pl. 229)

Range—Lower Oligocene of Peru (Chira formation).

Remarks—The few, heavy ribs and more or less angulate shoulder on the body whorl distinguish this *Harpa* from other species. The suture is covered by the appressed ends of the posterior ends of ribs, and the columellar and parietal callus is thin and spread to some extent over the body whorl. This species is therefore a true *Harpa*, and the earliest known species of this genus.

Through the cooperation of Dr. Katherine V. W. Palmer I have been able to examine the holotype, and have based the following description on this unique specimen.

Description—Shell rather small, 32 mm. (1¼ inches) in length, broadly and angulately ovate, spire broadly conical. Nuclear whorls lost, remaining whorls 4½. The antepenultimate whorl gently convex, with low widely separated ribs and a few fine spiral striae in the upper part of the interspaces. On the last half of the penultimate whorl (the surface of the earlier part is destroyed) there are two or three fine axial riblets (?growth lines) in the interspaces between the ribs which are slightly angulate at the shoulder; spiral striae are evident in the interspaces, and the lower third to a half of the whorl is covered by the adnate forward-curving upper ends of the ribs of the body whorl. The body whorl has nine strong ribs of which the last three are broader than the others; at the edge of the declivous subsutural ramp the ribs are angulate with an obtuse spine which is particularly apparent on the last four ribs; another pronounced angle is present below, giving the



Plate 229. *Harpa myrmia* Olsson, 1931. Lower Oligocene of Peru. 32 mm. (from Olsson, pl. 20, fig. 7).

shell a strongly shouldered appearance; the interspaces show again several strong axial striae, crossed by some more or less obscure spiral striae. Outer lip lost; ventral surface covered by a thin callus. Siphonal fasciole strong, lower end broken.

Length 31.9 mm., width 23.0 mm. Pal. Res. Inst. No. 2138, Chira formation, near Quercotilla, Chira valley, northern Peru.

Synonymy—

1931 *Harpa myrmia* Olsson, Bull. American Paleontology, vol. 17, no. 63, p. 114, pl. 20, fig. 7.

***Harpa* species**

A portion of a shell, found in the Lau Islands, eastern Fiji, is noted here in order to call attention to the presence of this genus in Lower Miocene times in eastern Melanesia. Although the ventral portion is missing, and the remaining portions of the penultimate and antepenultimate whorls are somewhat corroded, it appears that the

expanded portion of the upper ends of the ribs cover in some places about half of that part of the spire whorls between the shoulder angle and the suture. The ribs are fairly closely spaced, and are rather strongly angulate and sub spinose at the shoulder. I am therefore referring this specimen to the *Harpa*, making this one of the oldest representatives of the genus.

Judging from the size of the fragment, the complete shell would measure about 40 mm. in length, close to the maximum size known in *Eocithara*.

It is larger, with a more rounded, less angulate shoulder, than the Indonesian *E. muticaeformis* Martin of the same age.

The shell was collected in tuffaceous limestone on the coast between Tumbou and Tarakua-wai, Lakemba, Lau Islands, Fiji (H. S. Ladd, collector, Sta. L. 389). This is assigned to the base of the Futuna limestone and falls in stage *f* of the Lower Miocene (Ladd and Hoffmeister, 1945, pp. 25, 99, and personal communication).

Genus *Austroharpa* Finlay, 1931

This genus comprises a series of relatively small recent and fossil species from Australia. The adult shells range in size from 20 to 50 mm. in length, and are characterized by a large paucispiral bulbous or dome-shaped protoconch, and axial ribs whose upper ends are only slightly curved forward and hardly visible at the suture. The parietal callus is small but distinct and conspicuously margined, though the outer edge may not be raised or thickened.

I am dividing this genus into two subgenera, *Austroharpa* s.s. and *Palamharpa* Iredale, 1931, largely on the basis of the protoconch, that of the type species of *Austroharpa*, *A. pulligera* (Tate, 1889), being larger, bulbous and apparently tilted, while the species of *Palamharpa* have a smaller, dome-shaped nucleus with the suture marking the earliest whorl being horizontal. In addition *A. pulligera* is larger, 50 mm. in length, while most of the species of *Palamharpa* do not, to my knowledge, reach 40 mm. in length.

Subgenus *Austroharpa* Finlay, 1931

Type: *Harpa pulligera* Tate, 1889

This Middle Miocene subgenus contains only the single species *Austroharpa pulligera* (Tate, 1889) and is characterized, as mentioned above, by the large bulbous nucleus which seems to be tilted and quite different in appearance from the smaller, evenly dome-shaped protoconch of the species I am placing under *Palamharpa*. Because

of this striking character and relatively larger shell-size I am inclined to keep it distinct, especially since it was apparently living with a species, of the subgenus *Palamharpa*, *Austroharpa (Palamharpa) spirata* (Tate, 1889), both being found together in the same Balcombe Clay at Balcombe Bay, Victoria. This suggests that we are dealing with two distinct stocks, whose phylogenetic relationship can only be elucidated by the future discovery of related forms.

Synonymy—

1931 *Austroharpa* Finlay, Trans. New Zealand Inst., vol. 62, pt. 1 (May 31), p. 13.

Austroharpa pulligera (Tate, 1889)

(Pls. 231, 232)

Range—Middle Miocene (Balcombian) of Victoria.

Remarks—This is apparently a rare species, distinct by its size, relatively large among the species of this genus *Austroharpa* in length, its cassid-like form, and large, bulbous protoconch. The type, from Schnapper Point, near Morrongton, Victoria, north of Balcombe Bay, measures 50 mm in length; Dr. Thomas A. Darragh (in litt.) informs me that the National Museum of Victoria has eight specimens from Balcombe Bay ranging in length from 38 to 46 mm. He states that the species occurs also at Muddy Creek, near Hamilton, Victoria. As I have not seen specimens I am copying Tate's description:

Shell thin, oval, with a rather short spire, ending in a very large hemispheric pullus, with the tip laterally immersed; the second turn of the pullus almost concealed by the first ordinary whorl. Ordinary whorls one and a half, subangulated; ornamented with thin, slightly elevated lamellae,

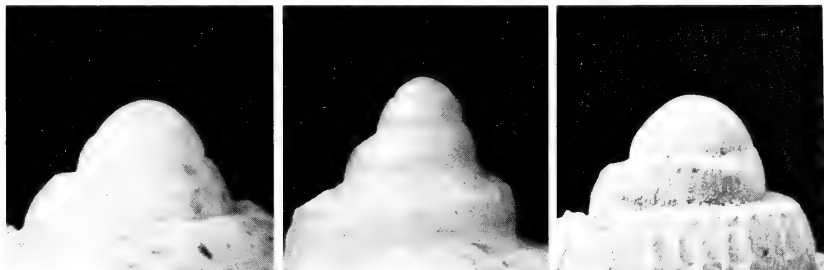


Plate 230. Enlarged protoconchs of species of *Austroharpa* (*Palamharpa*). Fig. 1. *A. (P.) punctata* (Verco). Off Venus Bay, South Australia, USNM 706971. Fig. 2. *A. (P.) exquisita* (Ire-

dale). off Burleigh Heads, Queensland, ANSP 314410. Fig. 3. *A. (P.) sulcosa* (Tate). Miocene, Hamilton, Victoria, USNM 157219. (all X 10).



Plate 231. *Austroharpa pulligera* (Tate). Holotype, 50 mm. in length. South Australian Museum, Tate Colln. 703.

which are vaulted on the angulation. Last whorl oval-oblong, somewhat ventricose over the suture, ornamented with about 25 thin, slightly elevated lamellae, which are raised into vaulted scales on the shoulder; the interspaces with coarse axial

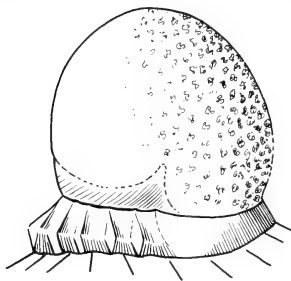


Plate 232. Protoconch of *Austroharpa* (*Austroharpa*) *pulligera* (Tate, 1889). (from Cotton and Woods, 1933, p. 46, fig. 8) X 7.5.

striae; base spirally wrinkled. Aperture narrow-oval; outer lip slightly ascending on the penultimate whorl, its margin much thickened.

Dimensions (in mm.)—length, 50, breadth 30, length of aperture 42, diameter of pullus 4.5.

Synonymy—

- 1889 *Harpa pulligera* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 151, pl. 6, fig. 9 (Blue clays at Schnapper Point, Mornington, Victoria).
- 1913 *Harpa* (*Eocithara*) *pulligera* Tate, Verco, Trans. Royal Soc. South Australia, vol. 37, p. 447.
- 1931 *Austroharpa pulligera* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 13.
- 1931 *Deniharpa pulligera* Tate, Iredale, Rec. Australian Mus., vol. 18, p. 230.

Remarks—This small, deepwater species was once considered, after *A. (P.) punctata* (Verco), the rarest of the harp shells. It is still uncommon in collections but has been brought up in recent years from moderately deep waters off southern

Subgenus *Palamharpa* Iredale, 1931

Type: *Palamharpa exquisita* Iredale, 1931

This group of recent and fossil Australian species is characterized by its rounded, dome-shaped paucispiral protoconch (1½ whorls), generally small size—from 20 to 35 mm. (the exception is a specimen reconstructed from a fragment of *Austroharpa (Palamharpa) loisae* Rehder which measures 45.8 mm. in length). In sculpture the species are very variable ranging from those with rather crowded lamellar ribs and cancellate sculpture through ones with very little or no spiral sculpture to a smooth species with only weakly indicated, widely separated, axial ribs. The recent species have a rather distinct notch at the upper end of the outer lip below its junction with the suture, which is not apparent in the fossil species.

This subgenus has been considered by some (Cotton and Woods, 1933, p. 47; Wenz, 1943, p. 1310) to be a synonym of *Austroharpa* s.s., but I believe that the striking difference in the protoconch is sufficiently important to warrant for the present their separation. In the many specimens of Harpidae, recent and fossil, that I have examined I have found the protoconchs to be quite constant.

The living species of the subgenus *Palamharpa* are found in moderately deep water from southern Queensland southward around the southern Australian coast to off Perth, Western Australia.

The fossil species range from Upper Oligocene to Upper Pliocene.

Synonymy—

1931 *Palamharpa* Iredale, Rec. Australian Museum, vol. 18, no. 4 (June 29), pp. 230, 233 (type, by original designation: *Palamharpa exquisita* Iredale).

1931 *Deniharpa* Iredale, *ibid.* (Type, by original designation: *Harpa clathrata* Tate).

1931 *Tramcharpa* Iredale, *ibid.* (type, by original designation: *Harpa spirata* Tate).

Austroharpa exquisita (Iredale, 1931)

(Pl. 230, fig. 2; Pls. 233, 237, figs. 4, 5)

Range—From off Burleigh Heads, southern Queensland, to Bass Straits, Victoria and Tasmania, in 25 to 80 fathoms.

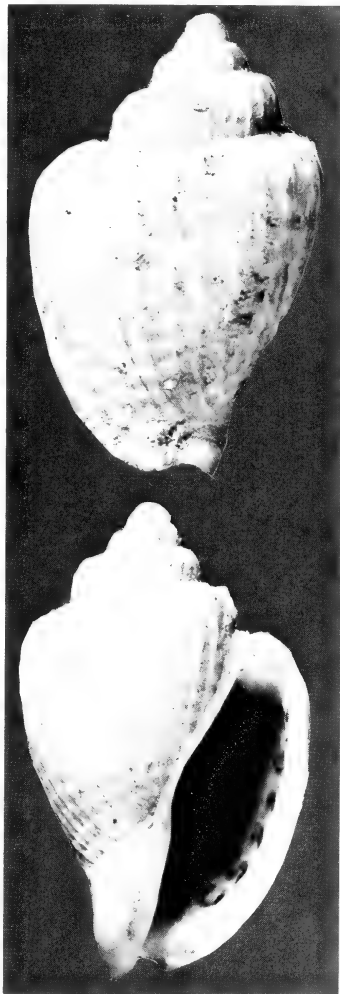


Plate 233. *Austroharpa (Palamharpa) exquisita* (Iredale). Holotype, Australian Museum no. C. 57753, from off Twofold Bay, New South Wales, Australia.

New South Wales and eastern Victoria by commercial fishermen; in the latter locality, according to Mrs. M. C. Griffiths of Lakes Entrance, Victoria, about 10 specimens have been found in the last thirteen years.

Habitat—According to Mrs. M. C. Griffiths (in litt.), specimens of this species are dredged in Bass Straits in an area about 7-9 miles ESE of Lakes Entrance, Victoria, on a bottom consisting of dead shell debris that formed almost a coarse shell sand.

Description—Shell small, 24-29 mm. in length, broadly ovate with a conical, turritid spire. Protoconch dome-shaped, of 1½ smooth whorls, the earliest part of the first whorl low and well immersed below the horizontal suture in succeeding whorl, last part more convex and impressed at suture; postnuclear whorls of spire with an increasingly angled shoulder, weak distant ribs, and broad low, obscure ridges, one in subsutural ramp, one at shoulder and two below the shoulder; the angulate shoulder and flattened subsutural ramp gives the spire a turritid appearance; between the ribs which become increasingly sublamellar, are numerous axial ridges, about 3 to 6. Body whorl strongly angulate, with about 22 to 27 low, sublamellar axial riblets which are rendered weakly scalloped by the broad, rounded spiral ridges they cross; these spiral ridges number 10-12 below the shoulder; the fine axial ridges between the ribs are sharply and finely sublamellar. Color of nucleus yellowish-pink, of body whorl from pale yellowish pink or moderate yellowish pink to dark orange yellow, with splotches of moderate reddish orange or grayish reddish orange on the subsutural ramp or arranged in obscure bands on body whorl, the spots darker on the lamellar ribs where they cross the spiral ridges. Aperture elongate, inner edge rather straight; outer lip gently arcuate, slightly flattened in center, somewhat flaring, thickened externally, with a definite notch below its junction with the body whorl; parietal-columellar junction indistinctly angulate, parietal callus narrow, distinctly margined, raised in the area of the base of the body whorl and the siphonal fasciole; siphonal canal rather deep and directed upward.

The soft parts of a specimen from Twofold Bay, New South Wales, sent to me by Dr. D. F. McMichael, then at the Australian Museum, Sydney, preserved in alcohol for some time, show an animal of which the propodium and head and anterior part of the metapodium are without spots; the posterior portion shows spots which are densest at the posterior end.

Measurements (mm.)—

length	width	no. whorls	
24	15	5	Holotype, Twofold Bay, N.S.W.
28.4	17	5+	Burleigh Heads, Queensland
29.0	17.3	5	Lakes Entrance, Victoria
21.7	12.5	5	Eden, New South Wales

Synonymy—

- 1931 *Palamharpa exquisita* Iredale, Rec. Australian Mus., vol. 18, no. 4 (June 29), p. 230, pl. 22, fig. 8.
 1933 *Austroharpa exquisita* Iredale, Cotton and Woods, Rec. South Australian Mus., vol. 5, p. 47; 1962 Macpherson and Gabriel, Marine Molluscs of Victoria, p. 215, figure 257; 1971 Wilson and Gillett, Australian Shells, p. 110, pl. 72, fig. 6.

Types—The holotype is in the Australian Museum, No. C. 57753, and the type locality, which was not mentioned by Iredale, is off Twofold Bay, New South Wales, in 45 fms.

Records—QUEENSLAND: off Burleigh Heads, in 34 fms. (ANSP). NEW SOUTH WALES: 11 mi W of Crowdy Head, in 50 fms. (AMS); E of Sidney, in 40-82 fms. (AMS); off Crookhaven Bight, in 30-35 fms. (Colln. W. A. Trenerry); Ulladulla (Colln. G. Thornley); off Crabo Id., Twofold Bay, in 50 fms. (AMS); off Twofold Bay, in 45 fms. (AMS, NMV); off Eden, in 50-60 fms. (USNM). VICTORIA: off Hospital Creek, in 30-60 fms.; ESE of Lakes Entrance, in 21-26 fms. (both Colln. M. C. Griffiths); off Lake Tyers (Collns. C. J. Gabriel, W. S. Ayres). TASMANIA: off Deal Id., Kent Group, Bass Straits, in 33 fms. (Garrard, 1961).

Austroharpa loisae Rehder, new species

(Pl. 237, figs. 3, 6)

Range—From WSW of Cape Naturaliste to NW of Rottnest Island, Western Australia.

Remarks—This strikingly sculptured species is most closely related to *A. (P.) exquisita* (Iredale) from the southeastern coast of Australia. It differs, however, in being more slender, not as strongly shouldered, in the axial and spiral sculpture being stronger and more regular, and in the protoconch and early whorls being lemon yellow rather than pinkish yellow in color.

A fragment of a large specimen found in 80 fathoms NW of Rottnest Island (SAM 34-70) is the basis for the maximum size mentioned in the description and listed in the measurements below. The height of the penultimate whorl, measured from suture to suture, was compared with the same measurement taken from the holotype; the relationship between these two measurements was equated with the total length of the holotype, and by this means an estimated length for the large specimen was determined.

The holotype has been figured by Wilson and Gillett in their book "Australian Shells" (1971, pl. 72, fig. 6a) as *Austroharpa exquisita* Iredale,



Plate 234. Geographic distribution of: 1, *Austroharpa (Palamharpa) exquisita* (Iredale), and 2, *Austroharpa (Palamharpa) loisae* Rehder, new species.

who noted that this form may prove to be a distinct subspecies or species.

This beautiful species is named for my wife in appreciation of her ever willing assistance, encouragement, and understanding.

Habitat—This species has been dredged from depths of from 70 to 103 fathoms, on sandy bottom with sponge and bryozoa.

Description—Shell of medium to relatively large size, thin, adults measuring from 28.4 to 45.8 mm. (1 $\frac{1}{4}$ to 1 $\frac{3}{4}$ inches), ovate, with a rather elevated, conical, and turreted spire. Protoconch almost hemispherical, dome-shaped, paucispiral, of 1 $\frac{1}{2}$ + smooth whorls, moderate yellow in color. Post-nuclear whorls $\frac{3}{4}$ in number, the obtuse shoulder marked by a spiral cord, in addition to which there is an obscure spiral cord on the subsutural ramp and more pronounced equidistant spiral cords below the shoulder (3 on the antepenultimate whorl, and 4 on the penultimate whorl). Crossing these cords are thin, rather distant, raised lamellar ribs (25 in the penultimate and 29 on the last whorl); these ribs are noticeably scalloped where they cross the equidistant spiral cords, the scallops being highest on the shoulder and subsutural cords; if the body whorl is viewed against a light, the axial ribs and cords make a very regular, reticulated pattern; between the axial ribs are 6 to 10 very fine, rather regular and somewhat separated, lamellar axial riblets. Color is a pinkish white or yellowish white to a yellowish gray, with the protoconch and first postnuclear whorls a moderate yellow; there are numerous small reddish brown spots where the ribs cross the cords, most noticeable on the abapertural side of the lamellar ribs, and occasionally a few larger spots of pale reddish brown on the subsutural ramp.

Aperture elongate, semilunate, with inner lip only slightly angled at juncture of parietal and columellar portions, and outer lip gently arcuate, somewhat broadly reflected and a little thickened internally, a small but distinct notch present at upper end below junction with body whorl; parietal callus thin, allowing sculpture underneath to be apparent, well margined, with a pronounced margin in adult shells; anteriorly, in the region of the well-developed and strongly lamellate siphonal fasciole, the margin is suberect, resulting in a noticeable pseudumbilical chink; anterior siphon rather deep, upturned.

Measurements (mm.)—

length	width	no. whorls	
28.9	16.7	5	Holotype
28.4	16.8	4 $\frac{1}{2}$	Paratype No. 1
45.8*	—	—	Paratype No. 3
36.4*	—	—	Paratype No. 4

*length (approximate) computed from height of penultimate whorl.

Synonymy—

1971 *Austroharpa exquisita* Iredale, Wilson and Gillett, Australian Shells, p. 110 (in part), pl. 72, fig. 6a. Not *Palamharpa exquisita* Iredale, 1931.

Types and Records—WESTERN AUSTRALIA: WSW of Cape Naturaliste, in 75 fms., broken shell (paratype no. 4, WAM 129-63); W of Rottnest Id., in 60 fms. (WAM 156-72); NW of Rottnest Id., in 70 fms. (holotype, WAM 1784-69); NW of Rottnest Id., in 100-103 fms. (paratype no. 1, WAM 31-64); NW of Rottnest Id., in 85 to 95 fms. (paratype no. 2 and fragment, WAM 127/128-63); NW of Rottnest Id., in 80 fms. (fragment, paratype no. 3, WAM 34-70); WSW of Dongara, in 60 fms. (paratype, USNM 707703; WAM 158-72; WAM 159-72); NW of Bluff Point, in 60 fms. (WAM 157-72).

Austroharpa punctata (Verco, 1896)

(Pl. 230, fig. 1; Pls. 235, 236)

Range—The eastern half of the Great Australian Bight, South Australia, from Nuyts Archipelago to Encounter Bay.

Remarks—This striking shell was the first of the living members of this genus to be described, and is still one of the rarest and most sought-after shells; only about twenty specimens are known. It is characterized by its size, relatively large for the subgenus, its inflated shape, and its smooth colored shell which is without any obvious spiral sculpture and has only low, obscure varices with a groove immediately in front of them and marked by scales on the subsutural ramp. It is quite distinct from any other known species, its closest relative being the smaller, more strongly sculptured species *A. (P.) wilsoni* Rehder described below.

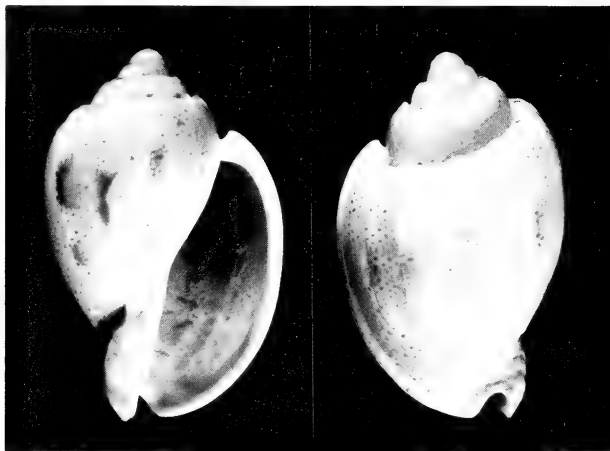


Plate 235. *Austroharpa (Palamharpa) punctata* (Verco). Holotype. South Australian Museum D. 13516. Off Newland Head, Encounter Bay, South Australia, in 20 fathoms.

Description—Shell moderately large, 32 to 36.3 mm. in length, inflated-ovate, with short, broadly conical spire, the whorls of which are flattened subsuturally and are convex below the rounded, not angulate shoulder. Protoconch rather large, hemispherical, dome-shaped, of $1\frac{1}{2}$ smooth whorls, the initial $1\frac{1}{2}$ whorls microscopically granulose. Postnuclear whorls $2\frac{3}{4}$ in number, convex, with a flat subsutural shelf, marked by low axial varices which gradually increase in strength; the varices are the outer edges of former lips, with the succeeding shell growth starting below the level of that non-reflected lip-edge, forming in this way a series of distant, overhanging steps, which are highest near the shoulder and gradually diminish in height towards the base; above the rounded shoulder and on the subsutural shelf the varices are marked by large, erect, forward-leaning, concave scales; between the varices the shell is smooth except for irregular, microscopic wavy striae. Color of protoconch and spire whorls a moderate yellowish orange-pink, body whorl varying from a moderate or strong yellowish pink to occasionally a deep yellowish pink or salmon color, with obscure bands and irregular spots of white; the darker, strong yellowish pink color may be patterned as large spots arranged in three bands—on the subsutural shelf and on the middle and lower half of the body whorl; the whole shell

is usually marked with irregular flecks and spots of various shades of reddish brown, the spots of various sizes and shapes but most frequently triangular, elongate, or sagittate; specimens are occasionally found without spots. Aperture elongate, semilunate, outer lip gently arcuate, rather broadly reflected, only slightly thickened externally and internally, inner surface showing the pink coloration of the external, obscure, darker banding; a strong triangular notch is present at the upper end, at the junction with the parietal wall. Parietal callus small, very thin, with the outer margin obscure; columellar callus with a conspicuous, thickened margin at the siphonal fasciole; siphonal canal short, deep, upturned.

According to a note by the collector of a living specimen from Thorny Passage, the animal is pale orange. The dried soft parts extracted from a specimen from Venus Bay (USNM 706971), and softened in Aerosol O.T., show scattered spots of reddish brown on a pale ground on both foot and tentacles; the siphon is also spotted and indistinctly annulate.

Measurements (mm.)—

length	width	no. whorls	
34.0	22.0	$4\frac{1}{2}$	Holotype, SAM D13516
32.5	21.5	$4\frac{1}{2}$	Paratype, SAM D459
35.0	24.0	$4\frac{1}{2}$	SAM D460
34.8	24.9	$4\frac{1}{2}$	USNM 706971
34.7	25.1	$4\frac{1}{2}$	Colln. Hurrell
36.4	24.9	$4\frac{1}{2}$	Colln. Delaney
31.9	21.4	$4\frac{1}{2}$	Colln. Delaney



Plate 236. *Austroharpa (Palamharpa) punctata* (Verco). Left fig. off Venus Bay, South Australia, USNM 706971. Center fig. off Encounter Bay, South Australia, Colln. S. T. Delaney. Right fig. off Venus Bay, South Australia, Colln. D. Hurrell. (all natural size).

Synonymy—

- 1896 *Harpa punctata* Verco, Trans. Royal Soc. South Australia, vol. 20, p. 218, pl. 6, figs. 3, 3a, 3b (Newland Head, South Australia).
 1913 *Harpa (Eocithara) punctata* Verco, Trans. Royal Soc. South Australia, vol. 37, pp. 446-447.
 1931 *Austroharpa punctata* Verco, Finlay, Trans. New Zealand Inst., vol. 62, p. 13; 1933, Cotton and Woods, Rec. South Australian Museum, vol. 5, p. 47; 1971, Wilson and Gillett, Australian Shells, p. 110, pl. 72, figs. 5, 5a.

Types—The holotype (SAM D13516) and paratype (SAM D459) are in the South Australian Museum. The type locality is off Newland Head, at the northern end of Encounter Bay, South Australia, in 20 fathoms.

Records—SOUTH AUSTRALIA: St. Francis Id., Nuyts Archipelago (SAM D460); off Venus Bay, in 27 fms. (USNM, Colln. D. Hurrell); near Port Lincoln (fide H. M. Laws); Thorny Passage, in 65 to 70 ft. (Colln. S. T. Delaney); Emu Bay, Kangaroo Id. (Colln. F. L. Saunders, fide H. M. Laws); American River, Kangaroo Id. (teste Verco, 1913); Backstairs Passage, in 22 fms. (teste Verco, 1896); Normanville (SAM); off Newland Head, Encounter Bay, in 20 fms. (holotype, SAM); Encounter Bay, in 20 fms. (SAM, Colln. S. T. Delaney).

Austroharpa wilsoni Rehder, new species

(Pl. 237, figs. 1, 2)

Range—From off Cape Leeuwin to off Dongara, Western Australia.

Remarks—This species is most closely related to *A. (P.) punctata* Verco by reason of its similar sculpture; it is, however smaller, more slender, with a relatively higher spire, and the shell a uniform whitish yellow with only occasional spots on the subsutural shoulder.

It is named for Barry R. Wilson of the Western Australian Museum, through whose generosity I

was able to study the Harpidae of Western Australia.

Habitat—All specimens were dredged in depths of from 60 to 120 fathoms on a sandy bottom, often with sponges, bryozoa, and starfish.

Description—Shell small, from about 20 to 25.7 mm. in length, thin, ovate, with an elevated conical spire. Protoconch, hemispherical, dome-shaped, of $1\frac{1}{4}$ whorls that appear smooth but are microscopically granulose; postnuclear whorls convex, with a very weakly angulate shoulder, and a slanted subsutural ramp; the sculpture consists of distant axial ribs, and in the earliest whorls a few low and broad spiral cords that gradually become obscure and are only very weakly indicated on the body whorl at and below the shoulder; in the early whorl the axial varices are more erect and rib-like, but later the varices are lower and have the appearance of low slightly overhanging steps; on the subsutural ramp the varices are more elevated and vaulted and occasionally form an erect, hollow triangular scale. The whole surface is superficially smooth but shows under highpower magnification very fine, obscure, wavy striae and coarser and irregular axial growth wrinkles. Color grayish yellow, occasionally with pale orange brown splotches on the shoulder and series of small light reddish brown spots on the varices behind the sharp edge; these seem to be arranged in spiral series, and on fresh shells a faint indication of spiral banding can be seen on the body whorl; the fine edge of the body-whorl varices shows a reddish brown color where these bands cross, and on the thickened edge of the outer lip the series of red brown blotches is conspicuous; these spots are continued on the inner edge of the thickened outer lip where in some instances the spots become a dark pink color; in dead shells the spots on the lip may disappear; in the holotype the siphonal fasciole is flushed with pink and the columellar callus

where it crosses the fasciole is a pale pink color. Aperture elongate-semilunate with outer lip gently arcuate, thickened internally, narrowly reflected, with a conspicuous, moderately deep sinus below its juncture with the parietal wall; parietal callus small, thin, the margin low but definite on the parietal wall, thickened on the columellar portion with narrow chinks above and below where it crosses the siphonal fasciole; siphon deep, upturned, its inner surface with a pale rosy flush. Wilson (in litt.) describes the living animal as "white with sparse lemon yellow spots on the sides of the foot and on the head, eye stalks lemon yellow, penis large and white."

Measurements (mm.)—

length	width	no. whorls	
25.3	14.7	5+	Holotype (WAM 36-70)
25.7	15.6	4½	Paratype No. 1 (WAM 125-63)
24.4	15.0	4½	Paratype No. 2 (USNM 703249)
22.8	14.1	4½	Paratype No. 3 (USNM 703250)
21.6	12.5	4½	Paratype No. 4 (WAM)
19.7	11.5	4½	Paratype No. 5 (WAM 35-70)

Types—The type locality is NW of Rottnest Island, off Perth, Western Australia in 80 fathoms on a bottom of sand with bryozoa and sponges; collected on a cruise of the "Bluefin," Sept. 15, 1965. The holotype is WAM 36-70.

Records—WESTERN AUSTRALIA: W of Cape Leeuwin, in 76-80 fms. (WAM 153-72); WNW of Cape Freycinet, in 107-129 fms. (WAM 154-72); W of Cape Naturaliste, in 96-100 fms. (WAM 155-72); SW of Garden Id., in 81-84 fms. (WAM 152-72); W of Rottnest Id., in 75 fms. (WAM 38-70); WNW of Rottnest Id., in 95-96 fms. (USNM 703250; WAM 122/124-63); NW of Rottnest Id., in 70-103 fms. (USNM 703249; WAM 35-70; 36-70; 125/126-63); WSW of Dongara, in 60 fms. (WAM 150-72); W of Dongara, in 80 fms. (WAM 151-72).

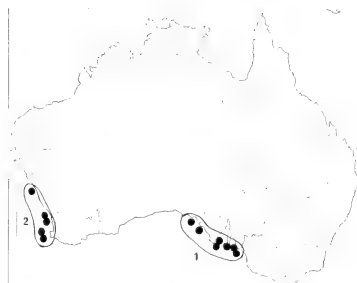


Plate 238. Geographic distribution of: 1, *Austroharpa (Palamharpa) punctata* (Verco), and 2, *Austroharpa (Palamharpa) wilsoni* Rehder, new species.

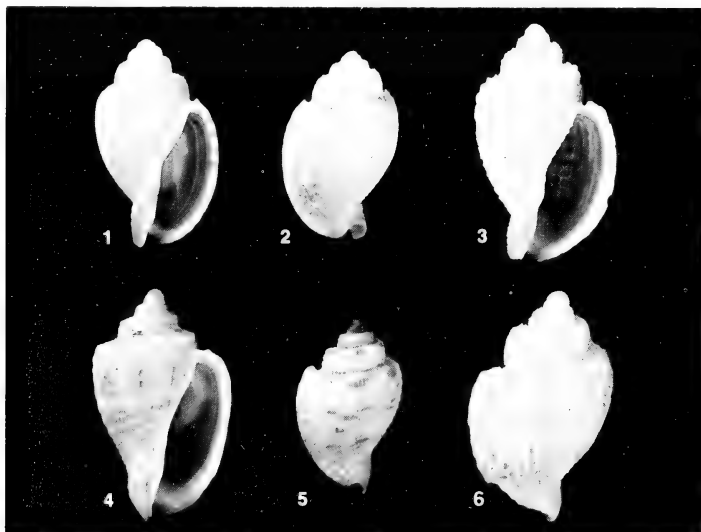


Plate 237. Figs. 1, 2, *Austroharpa (Palamharpa) wilsoni* Rehder, new species. 1, holotype, WAM 36-70. 2, paratype, WAM 123-62. Figs. 3, 6, *Austroharpa (Palamharpa) loisae* Rehder, new species. 3, holotype, WAM 178-69. 6, paratype, WAM

31-64. Figs. 4, 5, *Austroharpa (Palamharpa) exquisita* Iredale. 4, off Burleigh Heads, Queensland, ANSP 314410. 5, off Eden, New South Wales, USNM 634267. (all natural size).

Austroharpa sulcosa (Tate, 1889)

(Pl. 239)

Range—Middle Miocene (Balcombian) of Victoria.

Remarks—A species that seems closest to *A. (P.) exquisita* Iredale but with a lower spire, a somewhat more broadly ovate shape, and with stronger axial and spiral sculpture. The whorls are actually subsuturally canaliculate by the raised angular shoulder on which the axial ribs form erect lamellar and triangular scales. The parietal callus is thin judging from the single specimen with underdeveloped outer lip from the type locality I have been able to examine personally (USNM 157219); this specimen measures 28.2 mm. in length.

According to N. H. Ludbrook, this species is also found in the Fyansford Clay of the Balcombian at Shelford, Victoria.

Synonymy—

- 1889 *Harpa sulcosa* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 150, pl. 6, fig. 10 (Muddy Creek, Hamilton, Victoria).
 1897 *Harpa (Eocithara) sulcosa* Tate, Harris, Cat. Tert. Moll. Dept. Geol. British Museum, pt. 1, p. 79.
 1931 *Austroharpa sulcosa* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 13; 1933 Cotton and Woods, Rec. South Australian Mus., vol. 5, p. 47, fig. 2 (protoconch).
 1931 *Refluharpa sulcosa* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.

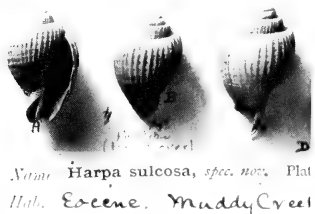


Plate 239. *Austroharpa (Palamharpa) sulcosa* (Tate). Holotype (28.2 mm. in length) and paratypes. South Australian Museum, Tate Colln. 718.

Austroharpa tatei Finlay, 1931

(Pl. 240)

Range—Pliocene (Dry Creek Sands) near Adelaide, South Australia.

Remarks—This species is close to *A. (P.) sulcosa* as Finlay and Ludbrook point out, and even more closely related to *A. (P.) loisae* Rehder of which it may represent an ancestral form. In number of

lamellate axial ribs on the body whorl (33) it is intermediate between *sulcosa*, which has about 38 and *loisae*, which has 29. It is less strongly angulate at the shoulder than *sulcosa*, lacks the spines at the shoulder, and the spiral sculpture is stronger. In all these features it is close to *A. (P.) loisae*. The type measures 25.5 mm. in length and 17 mm. in diameter. It is the Finlay Collection (no. 67) in the Auckland Museum, New Zealand.

Synonymy—

- 1931 *Austroharpa tatei* Finlay, Trans. New Zealand Inst., vol. 62, p. 14 ("Older Pliocene," Abbatoirs Bore, Adelaide, South Australia).
 1958 *Harpa (Austroharpa) tatei* Finlay, Ludbrook, Trans. Royal Soc. South Australia, vol. 81, p. 73, pl. 4, fig. 5.



Plate 240. *Austroharpa (Palamharpa) tatei* Finlay. Holotype. Auckland Institute and Museum. 25.5 mm. (copied from Ludbrook, 1958).

Austroharpa spirata (Tate, 1889)

(Pl. 241)

Range—Middle Miocene (Balcombian) of Victoria.

Remarks—This species is closely related to *sulcosa* Tate but has stronger sculpture, with the axial ribs broader and subequal and with more pronounced spiral cords, both resulting in a strongly fenestrated sculpture. Below the narrow

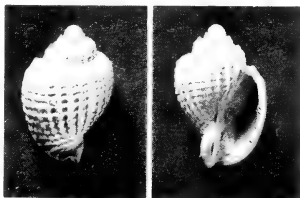


Plate 241. *Austroharpa (Palamharpa) spirata* (Tate). Shelford, Victoria. 26.5 mm. in length. South Australian Museum, P4257.

subsutural channel the subsutural ramp slants to the angulate shoulder, with the axial ribs bearing erect scales at the border of the narrow sutural channel.

The holotype of *A. (P.) spirata*, which measured 35 mm. in length has disappeared, according to N. H. Ludbrook, who has furnished the photograph which depicts a specimen from Shelford, Victoria.

Synonymy—

- 1889 *Harpa spirata* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 150, pl. 6, fig. 3 (Blue clays at Schnapper Point—Mornington, Victoria).
 1931 *Austroharpa spirata* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 13; 1933, Cotton and Woods, Rec. South Australian Mus., vol. 5, pp. 45, 47, fig. 3 (protoconch).
 1931 *Trameharpa spirata* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.

Austroharpa tenuis (Tate, 1889)

(Pls. 242, 243)

Range—Lower to Middle Miocene (Batesfordian to Balcombian) of Victoria.

Remarks—This species is larger than most of the other species and differs from the previous two species in the reduction of the spiral sculpture to low, more or less obscure ridges. It resembles in this respect the recent *A. (P.) exquisita* Iredale but

the latter has a higher spire, more angulately shouldered whorls, and the ribs are not spinose at the shoulder.

Besides the type locality of Muddy Creek, Hamilton, Victoria, this species is also found at Royal Park, Victoria in the Newport formation of the Balcombian (Middle Miocene), and from Flinders, Victoria, in the Batesfordian of the Lower Miocene.

The type according to Tate, measured 36 mm. in length and 23 mm. in width. A specimen in the collections of the USNM measures 36.2 in length and 21.7 mm. in width.

Synonymy—

- 1889 *Harpa tenuis* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 151, pl. 6, fig. 1 (Muddy Creek, Hamilton, Victoria).
 1897 *Harpa (Ecithara) tenuis* Tate, Harris, Cat. Tert. Moll. Dept. Geol. Brit. Mus., pt. 1, p. 80, pl. 4, figs. 4a, 4b (protoconch).
 1931 *Austroharpa tenuis* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 13; 1933, Cotton and Woods, Rec. South Australian Museum, vol. 5, p. 47, fig. 9 (protoconch).
 1931 *Deniharpa tenuis* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.

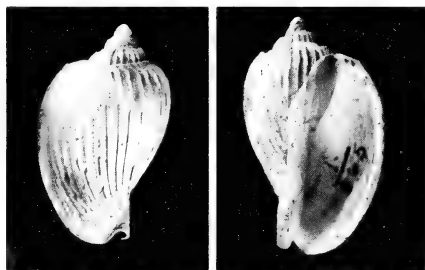


Plate 243. *Austroharpa (Palamharpa) tenuis* (Tate, 1889). Clifton, Victoria. Balcombian (Middle Miocene). USNM 647308. 36.2 mm.

Austroharpa abbreviata (Tate, 1889)

(Pl. 244)

Range—Middle Miocene (Balcombian) of Victoria.

Remarks—This species has a close resemblance in shape and nature of axial ribs to *A. (A.) pulligera* Tate, but differs in size and in the nature of the protoconch. It is fairly closely related to *A. (P.) tenuis* Tate but has fewer axial ribs, the whorls are not as strongly shouldered, the ribs do not bear the erect scales at the shoulder angulation, and the spiral sculpture appears to be absent or is at least very obscure.



Plate 242. *Austroharpa (Palamharpa) tenuis* (Tate). Holotype (34.5 mm. in length) and paratypes. South Australian Museum, Tate Colln. 702.



Plate 244. *Austroharpa (Palamharpa) abbreviata* (Tate). Holotype (27.5 mm. in length). South Australian Museum, Tate Colln. 710.

Synonymy—

- 1889 *Harpa abbreviata* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 150, pl. 6, fig. 7.
 1897 *Harpa (Eocithara) abbreviata* Tate, Harris, Cat. Tert. Moll. Dept. Geol. British Museum, p. 81, pl. 4, figs. 5a-b (protoconch).
 1931 *Austroharpa abbreviata* Finlay, Trans. New Zealand Inst., vol. 62, p. 13; 1933, Cotton and Woods, Rec. South Australian Museum, vol. 5, pp. 45, 47, fig. 7 (protoconch).
 1931 *Deniharpa abbreviata* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.

Austroharpa clathrata (Tate, 1889)

(Pl. 245)

Range—Lower Miocene (Batesfordian) of Victoria.

Remarks—This relatively large species is distinguished by the rather broad shell with a low conical spire, the fairly distant, narrow axial ribs crossed by strong subequidistant cords, the intersections at and just below the shoulder cord marked by subspinose nodes. The parietal callus is distinctly margined at its outer edge. The holotype measures about 39 mm.

Synonymy—

- 1889 *Harpa clathrata* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 151, pl. 6, fig. 8 (Murray River cliffs, near Morgan, South Australia).
 1931 *Austroharpa clathrata* Tate, Finlay, Trans. New Zealand Inst., vol. 13, p. 13; 1933, Cotton and Woods, Rec. South Australian Museum, vol. 5, p. 47, fig. 5 (protoconch).
 1931 *Deniharpa clathrata* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.

Austroharpa pachycheila (Tate, 1894)

(Pl. 246)

Range—Upper Oligocene (Janjukian/Longfordian) of Victoria.

Remarks—This and the following species, *A. (P.) cassinoides* Tate, were placed by Finlay (1931, p.

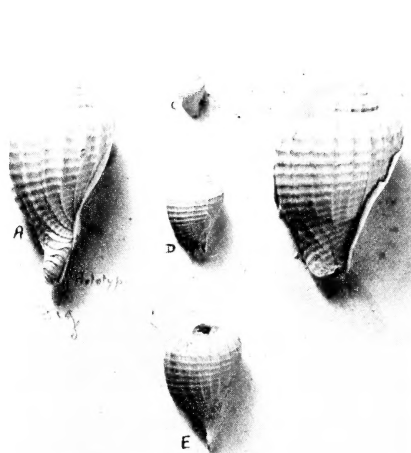


Plate 245. *Austroharpa (Palamharpa) clathrata* (Tate). Holotype (38.2 mm. in length) and paratypes. South Australian Museum, Tate Colln. 699.

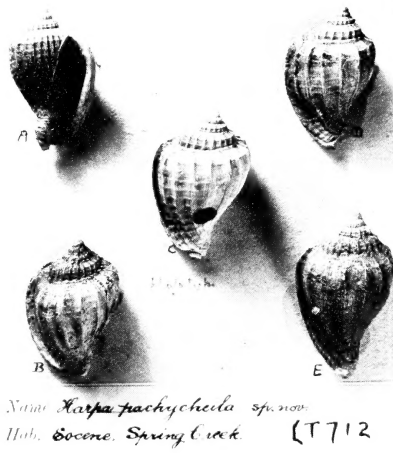


Plate 246. *Austroharpa (Palamharpa) pachycheila* (Tate). Holotype (at center: 27.5 mm. in length) and paratypes. South Australian Museum, Tate Colln. 712.

12) in the family Cassidae, "perhaps as *Oniscidia*," because of the character of the protoconch, and probably also because of their heavy "cassid" appearance. Three specimens of *pachycheila* are in the collections of the U.S. National Museum of Natural History, and all have a protoconch that is close to that found in the recent *Austroharpa* (*Palamharpa*) *exquisita* Iredale and related species, differing merely in being smaller, with a smaller initial whorl, and a somewhat more impressed suture; these appear to be differences of degree only. Drawings of the apical whorls of the holotype and paratypes of *pachycheila*, kindly sent me by Dr. N. H. Ludbrook, show that both kinds of protoconch are present in the type lot.

A. (P.) pachycheila Tate is a rather stout shell, strongly angulate at the shoulder, the ribs not lamellate but triangular in cross-section; in the first postnuclear whorl spiral cords crossing the axial ribs create a cancellate sculpture; the spiral cords diminish in strength, except for the one at the shoulder angle, particularly in the area below the shoulder. The outer lip is thickened and reflected, and the parietal callus is usually conspicuously marginate.

In general aspect and characters this species is close also to *A. (P.) clathrata* Tate.

The holotype measures 27.5 mm. in length. The three specimens mentioned above measure from 23.8 to 26.8 in length, and from 15.0 to 17.4 mm. in width.

Synonymy—

- 1894 *Harpa pachycheila* Tate, Jour. Royal Society New South Wales, vol. 27, p. 173, pl. 11, fig. 5 (Spring Creek—Torquay, Victoria).

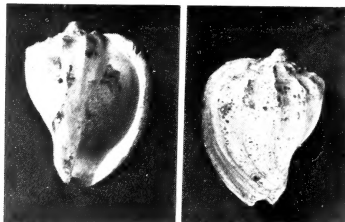


Plate 247. *Austroharpa* (*Palamharpa*) *cassinoides* (Tate). Holotype, 29 mm. in length. South Australian Museum, Tate Colln. 692.

- 1931 [*Oniscidia*] *pachycheila* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 12.
1931 *Deniharpa pachycheila* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.
1933 *Austroharpa pachycheila* Tate, Cotton and Woods, Rec. South Australian Museum, vol. 5, pp. 45, 47, fig. 6 (protoconch).

Austroharpa cassinoides (Tate, 1889)

(Pl. 247)

Range—Lower Pliocene (?) or Upper Miocene) to Upper Pliocene of New South Wales and South Australia.

Remarks—This species, together with *A. (P.) pachycheila* Tate and possibly also *A. (P.) clathrata* form a group of rather broad, angulate or subangulate, stout species with non-lamellar ribs, thickened, reflected lip that resemble in general appearance certain members of the Cassidae, and are rather dissimilar to most species of the living Harpidae. However, because their protoconchs approach those of more typical members of the subgenus *Austroharpa* (*Palamharpa*), and since most Australian workers, who have seen more material than I have, retain these species in this group, I follow their example.

This present species is the most aberrant of all members of this subgenus, and is characterized by its short, stout and broad shell, short spire, diminished number of strong non-lamellar ribs that are subnodose at the shoulder, lack of spiral sculpture, and a thickened, reflected outer lip, whose upper end is flexed upwards, projecting over the penultimate whorl to the antepenultimate whorl.

The type measures about 29.5 mm. in length and 22 mm. in width.

Synonymy—

- 1889 *Harpa cassinoides* Tate, Trans. Proc. Rep. Royal Soc. South Australia, vol. 11, p. 150, pl. 6, fig. 4 (Well sinking, Murray Desert—Tareena, New South Wales).
1931 [*Oniscidia*] *cassinoides* Tate, Finlay, Trans. New Zealand Inst., vol. 62, p. 12.
1931 *Deniharpa cassinoides* Tate, Iredale, Rec. Australian Museum, vol. 18, p. 230.
1933 *Austroharpa cassinoides* Tate, Cotton and Woods, Rec. South Australian Museum, vol. 5, p. 47, fig. 4 (protoconch).
1958 *Harpa* (*Austroharpa*) *cassinoides* Tate, Ludbrook, Trans. Royal Soc. South Australia, vol. 81, p. 74, pl. 4, fig. 4.

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